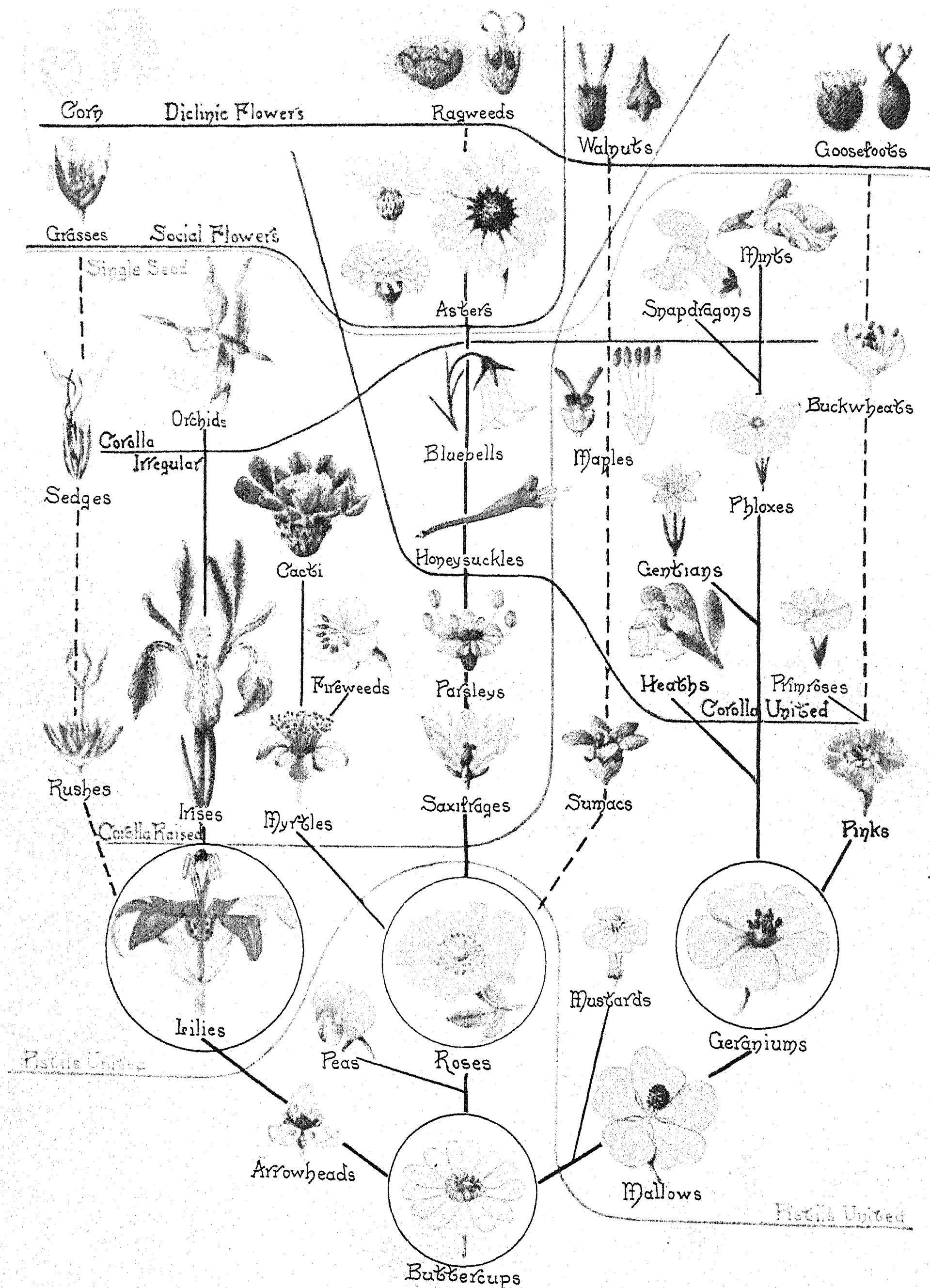

Courtesy The National Geographic Magazine

FLOWER CHART

FLOWER FAMILIES AND ANCESTORS

By

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THE H. W. WILSON COMPANY
NEW YORK
1928

Printed by the W. B. Conkey Company
Hammond, Indiana

PREFACE

THE chart method was originated in 1900 for the purpose of emphasizing the family type as a means of identification and of correspondingly reducing the difficulties of so-called "keys" for beginners. It was soon discovered that it possessed even greater value in portraying relationship and evolution, and this led to its continued elaboration for a quarter of a century. The chart originally made use of Bessey's treatment of the natural system, but further studies of pollination as the clue to the specialization of the flower resulted in many modifications, of which the treatment of the wind-pollinated lines was the most important.

After being employed in both elementary and advanced classes for eight years, the chart was condensed by omitting the families and was first published in the "Guide to the Spring Flowers of Minnesota" in 1908. With minor modifications it appeared in various editions of the "Guide," in "Minnesota Trees and Shrubs" (1912) and in "Rocky Mountain Flowers" (1913). In essentially its present form with the wind-pollinated phyla co-ordinate with the insect-pollinated ones, it was first published in Bergman's "Flora of North Dakota" (1917). A hand-painted wall-chart in colors was issued in 1921, and in reduced form this was published in the National Geographic Magazine for May, 1927. The chart has likewise served as the basis for Pool's "Families of Flowering Plants" (1928), and has been employed by Holman and Robbins in their "Textbook of General Botany" (2nd ed., 1927).

The present book has been written in the hope of making the study of flowering plants both simple and attractive to beginners of all ages. For this reason the use of technical terms has been avoided as far as possible throughout the text, and a short popular summary has been provided in the first section, under the heading of "The Family Tree." The hope is indulged that the main body of the text, though elementary, will serve the

purpose of interesting teachers of a wide variety of training and experience in the use of the chart method, and of acquainting instructors in systematic botany with a natural and dynamic approach to their field. While a comprehensive and detailed account of the natural system on this basis is in preparation, several years at least must elapse before its publication.

While an endeavor has been made to render the text both readable and interesting and hence no apology seems necessary for the occasional use of metaphor, it is hoped that the book will do more than afford an opportunity for *reading* about plants. If it does not provide the means by which the plant-lover can find his own way through garden and field, and the teacher can develop the spirit of inquiry in his students, it will have failed of its primary purpose.

Grateful acknowledgment is made of the courtesy of the National Geographic Society in permitting the use of the color chart and the original introduction to "The Wild Flowers of the West" (National Geographic Magazine, May, 1927). The illustrations for life-histories and pollination methods are slightly modified from Clements and Long, "Experimental Pollination," published by the Carnegie Institution of Washington. The major number of the text figures are from original drawings, but some have been drawn from the following authors, especially the first two: LeMaout and Decaisne, Mary Eaton, Eichler, Longyear, Bergen and Caldwell, Gray, Gager, Schröter, Sargent, Strasburger and Wettstein.

FREDERIC E. CLEMENTS.
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Mission Canyon
Santa Barbara
October 15, 1927

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SURPRISING as it may seem to think of primroses, lilies, bluebells, sweet-peas, sunflowers and maples as descendants of a single original flower form, the nature-lover soon comes to understand why this is so. The faces of flowers are much like those of people in bearing the impress of experience more or less plainly stamped upon them. The imprint is deeper, however, since plants are much more directly affected by their environment. It is also more significant, because flowers represent thousands of different species, while all the races of man

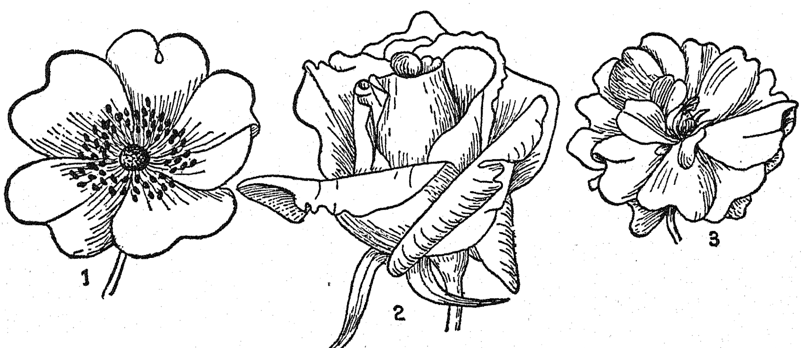

Fig. 1. Varieties of Roses
(1) Wild Rose; (2) Bridesmaid; (3) Edith Cavell

belong to but a single one. The individuals of one race or nation are more or less clearly set apart from those of another as a consequence of their common descent and environment, so that it is often possible not merely to recognize a man's race, but also in some cases to make a good guess as to his nationality.

With flowers this can be done much more easily and accurately. It is a matter of every-day knowledge in the case of the

many garden varieties of roses, tulips, petunias, verbenas, and a host of other flowers. The likeness is less obvious with different species of lily—tiger, Turks-cap and Bermuda—and the resemblances between lily, tulip, trillium, hyacinth, onion and Solomons-seal must be sought much more diligently. In other families the general resemblance may be even more elusive, and careful scrutiny is needed to disclose the fact that buttercups, anemones, marsh marigolds, clematis, peonies, columbines and larkspurs are at bottom enough alike to belong to the same family.

Fig. 2. Flowers of the Buttercup Family
(1) Buttercup; (2) Yellow Anemone; (3) Alpine Clematis; (4) Marsh-marigold; (5) Peony; (6) Blue Larkspur; (7) Red Columbine

Even more clearly than with animals, plants are the product of their environment, and it demands no great clairvoyance to read their experiences in face and form. In the case of one generation this clue would be slight were it not for the tendency of plants to stay close at home, so that the offspring repeat the experiences of the parents until the stamp of the home environment becomes indelible. Water-lily pond-lily, and the fabled lotus of the Nile bear the mark of water in stem and floating

leaf, and of a simple tranquil mode of life in the many-petalled flowers. But with many first cousins among plants it is quite otherwise. Root, stem and leaf are fashioned by water, light, heat or drouth, while the flower is molded by bee or butterfly, the pull of gravity or the breath of the south wind, and the fruit shaped by its choice of conveyance, of wind, water, the pelt of a bear, or the trousers of a boy afield. The rose and its near relatives bear flowers easily recognized by their likeness, but the leaves are of many sorts, the stems may run, climb or stand straight and tall, and the fruits range from rose-hip or red-haw to strawberry, cherry, almond and apple. But through the maze of blood relationship runs the bright hue of the flower as the best guide to the deeper experience of the species and its ancestors in the remote past. More recent experiences have often been recorded in the fruits, and those of yesterday have left their mark on stems and leaves.

In essentials, the experiences of plants do not differ so much from those of animals and man. Each is a series of adjustments to environment, of successes and failures in solving the problems of existence. From plant and flower can be learned many lessons of value for our own guidance, and this is truest of all in matters that have to do with the control exerted by environment in human affairs. In so many ways their problems are much more like our own than would seem possible. Rain and drouth, heat and cold, sun and cloud act upon them in the most intimate fashion. They can modify their environment, or they can leave and move into another one, sometimes when grown up, but usually as tiny seed children securely wrapped up from harm and supplied with proper food. Some plants even control the environment in a striking degree, especially when they co-operate as trees do in a forest or grasses in a lush meadow. They also compete with each other for the things they need, the rewards of success being quite as decisive as among men and the penalty for failure even more severe. As the manufacturers of food for the whole world of living things, plants have a unique rôle, but as consumers they possess many habits in common with animals and men. Significant of this relation is the fact that man the world over

obtains his chief food supply, starch, by taking it away from the plant babies found in the seeds of wheat, oats, rice, corn and their relatives.

Overtime and Emergencies

Since plants must make all of their own food as well as that of all other living things, their working day is a long one. Indeed, if they were to be paid for overtime at the regular rate, the prices of foodstuffs would again soar skyward. The manufacture of starch and sugar is a daylight job because the plant must use sunshine to drive its machines, but packing it away for the future in root and seed can just as well be done at night. This is likewise true of growing and various other tasks that depend upon prepared food for the necessary energy and not upon direct sunshine. In spite of its appearance of elegant ease, every plant works upon a 24-hour schedule, though some of the parts enjoy rest spells between times.

In addition to overtime, plants are often called upon for emergency work in repairing the ravages of insects or rusts, of wind and storm, and especially in adjusting themselves to new conditions. In many ways this last is the most interesting work they do, since out of it come the new and improved plants that bedeck our gardens, increase the yield of our fields, and enhance the charm of the country-side. The response that plants make to changing experiences is the one clue to their life-story and hence to the relationships to be traced in their features, all of which we term evolution.

To walk through a garden filled with many species is to be struck with their bewildering diversity, but a closer acquaintance reveals the harmony beneath the many forms. At first it seems incredible that thousands upon thousands of different flowers should be built on the same general plan, impossible that so few parts could yield such an endless variety of blossoms. But even the most intimate acquaintanceship can discover only four flower parts and but four ways of combining them to produce the characteristic flowers of several hundred families and thousands of genera.

As one of the four organs of the plant, the flower has its own special work to do, and in turn it sublets the various jobs to its four parts, calyx, corolla, stamens and pistils. In a sense, it takes the contract for making a certain number of good seeds and assumes the responsibility for handling its parts in such a way as to ensure this result. Seed-making is impossible without the transfer of pollen and the most interesting work of the flower centers about this indispensable process. The stamens manufacture the pollen grains, and the pistils bear the bodies that become seeds when fertilized by the pollen. But experience has taught flowers that a mere transfer of pollen is not enough. It is desirable and sometimes imperative that the transfer be made between two different flowers. The simple flowers of the

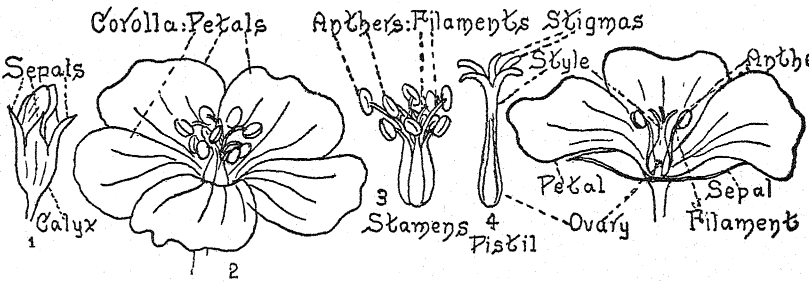

Fig. 3. Pattern Flower Showing the Four Parts
Geranium: (1) Bud; (2) Open Flower; (3) Group of Stamens; (4) Pistil; (5) Section of Flower

pines were the first to employ the wind as a transfer agent, but all our well-known flowers have turned to insects for this work. To attract these workers it was necessary to advertise, and as a result all such flowers hang out a brightly colored poster, the corolla, as a sign that nectar and pollen may be had within. The fourth member of the partnership is the calyx, which serves as a guard to the more delicate parts in the bud, and beguiles its leisure with small jobs of starch-making, as its green color suggests.

Efficiency Tests Among Flowers

When one asks what flowers were the first and hence the oldest, the best answer is those that are least skillful in securing

the transfer of pollen and the making of seeds, and least economical in the use of material and energy. The test is not so very different from those applied to men. In spite of his general usefulness, a "jack-of-all-trades" is much less satisfactory for a particular job than the man that specializes in doing one thing thoroughly well. So it is with flowers. The story of increasing efficiency is one of progressive specialization, and the highest and most recent of flowers are those most specialized and correspondingly efficient in seed-production.

The path taken by students of flower efficiency and relationship can easily be retraced by any interested nature-lover. Pluck a half dozen blossoms as unlike as possible and let each present the evidence of its skill—bluebell, buttercup, primrose, hollyhock, foxglove, lily and honeysuckle. The best test is afforded by the stamens and pistils, since these are directly concerned with pollen transfer. A large number of stamens means a high charge for transfer in terms of pollen eaten or wasted, while an excess of pistils means that many of them will fail of pollination, since the bee is not in the least concerned to see that each stigma is dusted. To unite parts is to save material for other needs, just as it is cheaper to build one house of several rooms than several houses of one room each. We shall also see that combining flowers in co-operative groups effects a great economy in both effort and material. By these and similar tests we discover that the buttercup order, comprising buttercups, anemones, larkspurs, magnolias, calycanths and many others, contains the simplest and lowest of flowers in the usual sense, while snapdragons, lobelias, and orchids are among the most specialized and highest of flowers pollinated by insects. Wind-pollinated flowers have naturally solved the problems of pollen transfer in a very different manner, but here too the most specialized are the highest.

At first thought it may well seem incredible that the buttercups as the simplest and oldest of flowers must be the ancestors of all the others. But even a general acquaintance with the various flowers of this order indicates that this is true. Not only do they meet all the requirements laid down for simple flowers, but likewise nearly all the changes found in the higher

families are foreshadowed by them in some degree. They have necessarily met with many and varied experiences, have solved pressing problems in various ways, and hence have anticipated most of the solutions later found by higher types. But nearly all these discoveries were lost, as not infrequently happens in human progress, and had again to be laboriously worked out as the flower advanced in experience and skill.

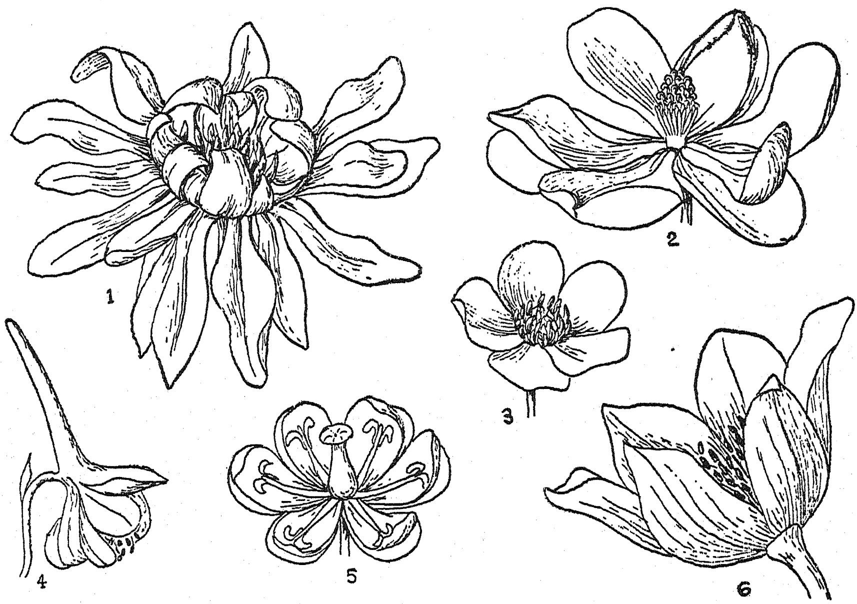

FIG. 4. THE SIMPLEST OR LOWEST FLOWERS
(1) Calycanthus; (2) Magnolia; (3) Swamp Buttercup; (4) Scarlet Larkspur; (5) Barberry; (6) Pulsatilla

PROBLEM SOLVING AMONG BUTTERCUPS

For a long time buttercups must have remained very uncertain as to the best number plan for the flower, since all plans from 10 or more to 3 or even 2 have been tried. The calyx and corolla were the first parts to know their own mind and to settle upon plans of 5, 4, or 3, which were henceforward to become the preferred number for the vast majority of their descendants. Progress was slower among the stamens and

pistils, and their numbers remain large in all but the most specialized buttercups. The difficulty in persuading bees to dust a myriad of separate pistils with pollen usually led to their more rapid disappearance, and the larkspur thus has but 2 or 3 pistils to a score or more of stamens. However, the mousetail has been much less efficient in this respect and still produces hundreds of pistils to a small number of stamens, with the result that many seeds never ripen.

Success in achieving pollen deposit thus depends upon many stamens, so that the bee may take his usurious toll of pollen, or upon furnishing a reward in the form of nectar. To produce the latter was a fairly simple task, but to protect it from

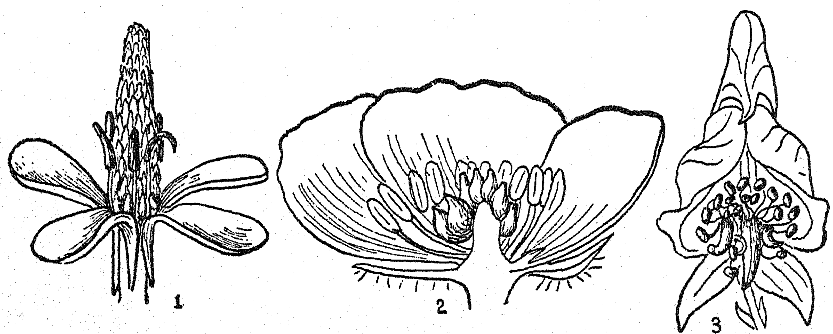

Fig. 5. Reduction in Number of Pistils in the Buttercup Family
(1) Mousetail; (2) Buttercup; (3) Monkshood

marauders as well as from rain demanded a new type of construction. Thus, the simple nectar pit on the petal was first provided with a scale for a roof and then the petal was more or less completely transformed into a special sack for nectar, such as we find in columbines, larkspurs and monkshoods. The problems to be solved in securing pollination were wholly different when wind was used as the transfer agent. Bright colors and a supply of sweets were of no avail with the wind, and in consequence petals and nectaries disappeared. The emphasis was put upon long threads to hang the anthers out on the breeze and plumy stigmas to catch the pollen as it floated past. This solution proved most feasible when the labor was divided, so

that meadow-rue and clematis thus came to have two kinds of flowers, one for making stamens and the other pistils.

How Buttercups Became Lilies

Though the conversion of buttercups to lilies must have taken a long time, the actual number of steps is not many. Indeed, the most striking feature of the lily flower is already found in those buttercups with a number plan of 3, a plan that more or less disguised is still found in the orchids and grasses. The flowers of arrowheads and water-plantains show no other

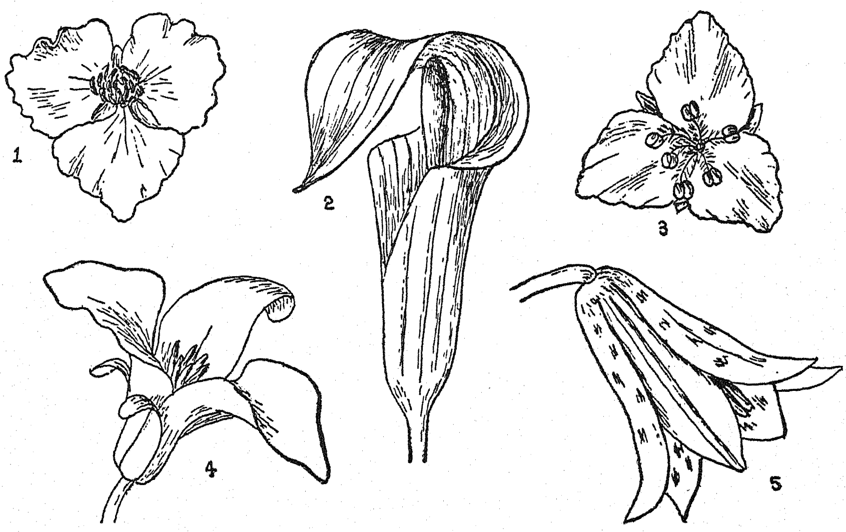

Fig. 6. Arrowheads, Arums and Lilies
(1) Arrowhead; (2) Jack-in-the-pulpit; (3) Spiderwort; (4) Trillium; (5) Thimble Lily

important difference from those of buttercups, but the plants have become lake-dwellers and have changed their stems and leaves accordingly. Some of their descendants became tired of the placid life in water, and ventured forth upon the land. Those that had lost the corolla requisitioned a leaf, painted it in bright colors and wrapped it around the naked flowers for protection and attraction, and thus became calla "lilies," jack-in-the-pulpits, and anthuriums. Others enlarged and brightened

the corolla, and united the pistils to secure better pollination with the use of less material. These became day-flowers and spiderworts, with a green calyx, blue or purple corolla, six stamens and three pistils in one. No further change of importance was needed to transform these into the trilliums or wake-robins, the simplest members of the lily family. However, the true lilies owe their beauty to an evident need for greater attraction. This has been secured by coloring the green calyx like the corolla, so that the latter appears to have six petals. This advance proved so successful that all the insect-pollinated descendants, snowdrop, daffodil, iris, and orchid, exhibit it, and its effects are to be traced through the wind-pollinated rushes and sedges to the grasses. Like the buttercups, the lilies too have made their own experiments, but they have been much more conservative as to their flowers. In spite of striking differences in color, shape and size, lilies of all sorts, tulips, mariposas, onions, hyacinths, aloes, asparagus, lily-of-the-valley, and yuccas are easily recognized as members of the same family.

How Buttercups Became Roses

Compared with the lilies which are only distant cousins at best, the roses may well be regarded as first cousins of the buttercups. Indeed, the simplest members of the rose family resemble the latter so closely that they are often mistaken for each other, while the raspberry and strawberry are to be distinguished from buttercups much more easily by their fruits than by their flowers. The resemblance lies in the number plan of 5, the many stamens and pistils, and the lack of union in the latter. The chief difference consists in the tendency of the calyx to form a cup that bears the petals and stamens on its edge, a change well shown in the apple. This cup not only serves to place the petals in a better position for attraction, but it likewise contributes to the formation of the fruit, making the brightly colored rose-hip and red-haw, and the thick flesh of apple, pear and quince. In fact, while roses undergo more or less reduction in the number of stamens and pistils as they do their work more efficiently, their flowers are much alike. However, their

fruits have developed in the most varied fashion, ranging from tiny seed-like ones in the cinq-foil to strawberry, raspberry, blackberry, red-haw, apple, pear, plum, peach, apricot, and

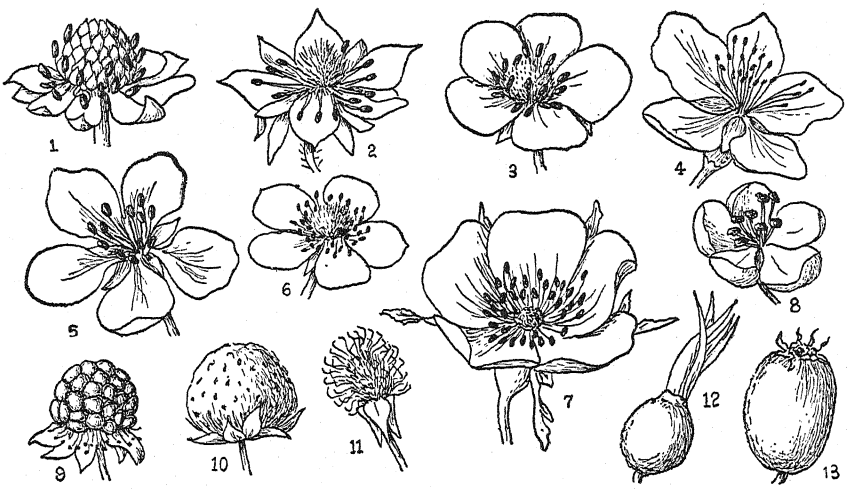

Fig. 7. Flowers of the Rose Family and Their Fruits
(1) Crowfoot; (2) Raspberry-blossom; (3) Strawberry-blossom; (4) Peach-blossom; (5) Pear-blossom; (6) Avens; (7) Sweet-briar; (8) Hawthorn; (9) Raspberry; (10) Strawberry; (11) Fruit of Avens; (12) Rose-hip; (13) Red-haw

almond, and such dry bur-like ones as are found in avens and agrimony.

How Buttercups Became Geraniums

The transformation of progressive buttercups into poppies and mallows took place so gradually that no sharp line can be drawn between them. The advantages of saving material and enhancing the certainty of pollination have been so decisive that the union of pistils into a compound one has been the ruling motive. But even this has been a slow process, and certain poppies and mallows still retain the separate pistils of the buttercups, while the fruits of the "cheeses" indicate that union is still incomplete in the mallows. Economy of effort and material has likewise led to more definite number plans, poppy architects inclining strongly to the plan of 4 and the mallows adhering

to that of 5. As usual, this is best seen in corolla and calyx, is less regular in the pistil, and is attained last in the stamens, where provision for waste is essential. Like the ancestral buttercups, the poppies too have experimented with division of labor in the corolla, producing the irregular flowers of the bleeding-heart and Dutchman's-breeches. In sweet alyssum and other mustards, this process has operated only on the stamens, yielding four long and two short ones, with consequent values for pollination.

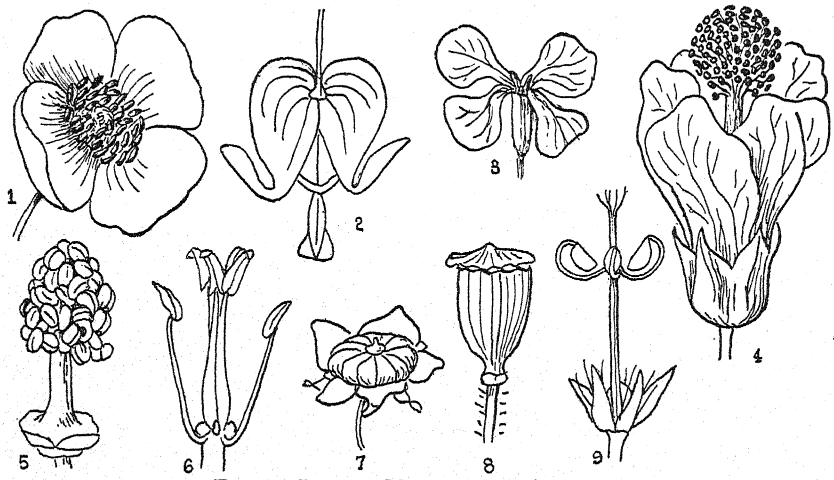

Fig. 8. Poppies, Mustards and Mallows

(1) Poppy; (2) Bleeding-heart; (3) Radish; (4) Abutilon; (5) Stamen-cluster of Mallow; (6) Stamens of Mustard; (7) Fruit of Mallow; (8) Poppy Capsule; (9) Fruit of Geranium

As a rule, the mallows have been more orthodox in their behavior. They much resemble poppies in their large corollas, the flowers of hibiscus and hollyhock being exceeded only by those of the oriental and Matilija poppies, but differ in the tall pillar of stamens and the fluted cheese-like fruits. In the flower of the linden, the stamens are arranged in five clusters, and these are reduced in the geraniums to two or three rows of five stamens each. The significance of this is seen in the reduction of the pistils to five, though the ancestral tendency is disclosed in their separating when ripe.

Geraniums and Their Kin

Even a professional geneologist might well find difficulty in tracing the kinship between geraniums and touch-me-nots, owing to the curious forms of the latter arising from division of labor and the fusion of parts. The ancestral symmetry of mallow and buttercup is found in the geraniums of meadow and woodland, but it is already being lost in the cultivated geraniums, which are properly called pelargoniums. In the simplest of these, the petals exhibit some uncertainty as to their proper position and form, and such species as the ivy and rose geraniums have taken a decisive step in the direction of dividing up the work of the corolla. The petals are arranged in groups with two above and three below, and these differ in their size, shape and markings, in addition to the presence of a sepal spur for nectar storage. When the petals become more unlike in response to the several tasks of attraction and guidance, and the spur drawn out into a long nectary, the pelargonium has become a nasturtium. This is the missing link between geraniums and the balsams or touch-me-nots, in which the flower is so irregular as to seem entirely unrelated. These have converted the spurred sepal into a large cornucopia at the expense of the other four, which are on the point of disappearing. In the competition between the petals, one has far outgrown the others, which have fused with it to make a flower puzzle.

Flax and oxalis are closely related to the geraniums, as well as to each other, but their later experiences have differed enough to make the one a highly prized crop plant and the other a lowly ornamental. In their chief features the flowers differ little from those of the geranium, but they depart from the parental habit in being day-bloomers, as well as in their pod-like fruits.

How Geraniums Became Mints

The line of descent from geraniums to mints is such a long one that the latter are to be accounted among the patricians of the flower world. They are the last and highest of the lineal descendants, a fact attested by their royal blues and purples,

and perhaps also by their fondness for perfumes. The improvement of the corolla for insect pollination is first marked by the union of the petals and then by their division of labor, as a result of which attraction, landing, guidance, and protection have been assigned to different parts. The increasing success of such specialization is reflected in the gradual reduction of the number of stamens and pistils, and especially in fewer and better seeds per flower.

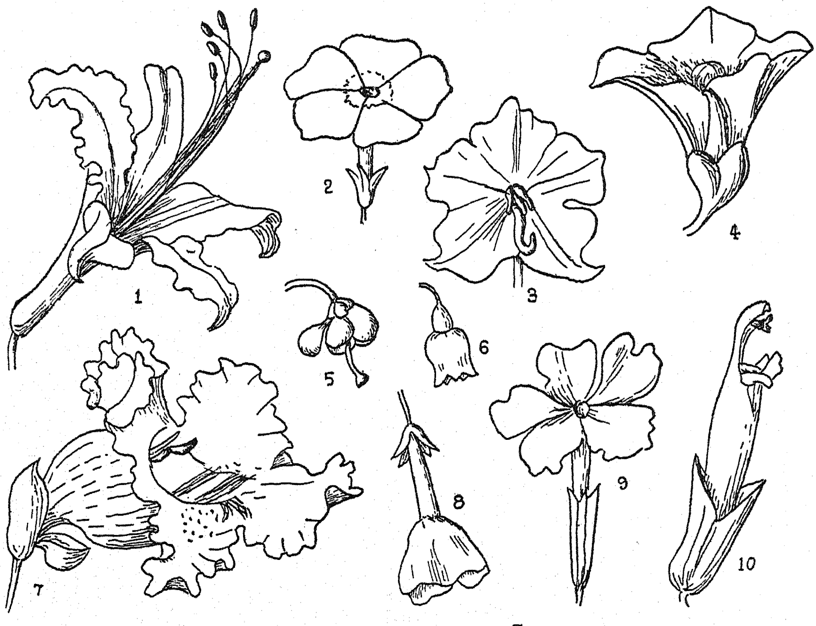

FIG. 9. THE DESCENDANTS OF GERANIUMS
(1) Azalea; (2) Phlox; (3) Buffalo-bur; (4) Bindweed; (5) Pink Pirola; (6) Box Blueberry; (7) Catalpa; (8) Mertensia; (9) Verbena; (10) Scarlet Sage

The immediate descendants of the geraniums and their relatives, the rues, are thought to be found in the pipsissewas and wintergreens, in which ancestral traits still persist in the double ring of stamens and in the number of pistils and the lobing of the ovary. The fusion of the petals and sepals has barely begun, but it proceeds rapidly in the other heaths, to become marked in the perfect bells of blueberry and heather. The union of the

corolla is universal in the next higher order, the phloxes, and is thenceforth a regular feature, though the degree varies much in different flowers. The simplest phloxes are built throughout on the number plan of 5, but the majority, including the potatoes and morning glories, compensate for the advance in the corolla by a corresponding reduction in the number of pistils, producing an ovary with but three or usually two cells. The gentians closely resemble the phloxes, but some members of the order, such as the milkweeds and ashes, have forsaken most of the ancestral customs in their far-reaching adjustment to new methods of pollination. A few members of the potato family have developed corollas with two lips, and these are the direct ancestors of a host of beautiful flowers—foxgloves, snapdragons, butter-and-eggs, trumpet-creepers, catalpas, etc.

The borage family, comprising heliotropes, forget-me-nots, mertensias, puccoons, and many others, passes almost imperceptibly into the verbenas and mints, indicating a close relationship between them. The change is from a regular flower with five stamens to an irregular one with but four or two, but the buglosses have two-lipped flowers and a few verbenas and mints possess nearly regular corollas. Even more significant is the fact that the three families exhibit the same solution of the problem of securing one-seeded fruits, with all the advantages that this entails. It would seem that the usual method of gradually reducing the ovary to a single cell and seed was too slow for the borages, and they made a short-cut by dividing the two cells to make four one-seeded nutlets. This device evidently proved as successful as the regular one, since it remains a characteristic feature of both verbenas and mints with their hundreds of species. The improvement of corolla and pistil exerted the usual effect upon the stamens, which have not only dwindled to two in the highest mints, such as the sages, but have also undergone a special modification to increase the efficiency of pollen-loading. Finally, the monardas and globularias have converted their flower clusters into co-operative communities, approaching in several respects the highly specialized community found in the sunflower, aster and dandelion.

How Geraniums Became Pinks and Buckwheats

The step from flax and oxalis to the pinks is but a short one, the flowers being essentially similar in their main features. A growing tendency toward the conservation of energy and material is expressed in the reduced number of pistils and the loss of cross-walls, as well as in the disappearance of the corolla and a turning to the wind as the agent of pollen transfer. Our garden pinks have also taken an interesting short-cut to secure the advantages of a united corolla by fusing the sepals into a tube. With the strong bias for experiment shown by the pink family, it is easily understood why this line is today one of the most active as to evolution, especially in response to wind-pollination.

The primroses and sea-lavenders have sprung from the pinks in one direction through the union of the petals, an advantage reflected in the loss of one row of stamens. In another direction have arisen the portulacas and spring-beauties, and in a third the tamarisks and their relatives, the willows and poplars. The latter best exemplify the ever-present trend toward wind-pollination, which in this case has led to the loss of corolla and calyx and a division of labor in the flower that man is learning to utilize. Since the stamens and pistils are borne on separate trees, showers of cotton can be avoided by planting the staminate tree alone. The plantains are at present in the very process of changing pollination agents. The anthers are hung out on thread-like filaments typical of wind-pollination, and the useless corolla is now tiny and colorless, almost on the point of vanishing. The significance of this in terms of efficiency and division of labor is seen in the fact that the highest plantains have two kinds of blossoms, the ovary is one-celled and the fruit contains but a single seed.

The main line of descent from the pinks leads to the buckwheats, four-o'clocks, amaranths and goosefoots, the last including the sugar-beet, chard and spinach. The apparent absence of flowers in most of these is explained by the loss of color and reduction of parts resulting from wind-pollination, which controls the destiny of these plants. The four-o'clocks and the

common buckwheat seem to have returned to the customs of their ancestors after the loss of the corolla. The calyx now does the work of the corolla, and with its bright color and store of nectar is the cynosure for humming-bird, sphinx-moth and honey-bee. A brilliant calyx also occurs in such amaranths as the cock's-comb and the globe-everlasting, but the tiny flowers are papery and nectarless and differ only in color from the green wind-flowers of the common pigweeds. In all of these, the flower has attained the goal of efficiency, which is the production of a tiny seed-like fruit containing a single plantlet, and in

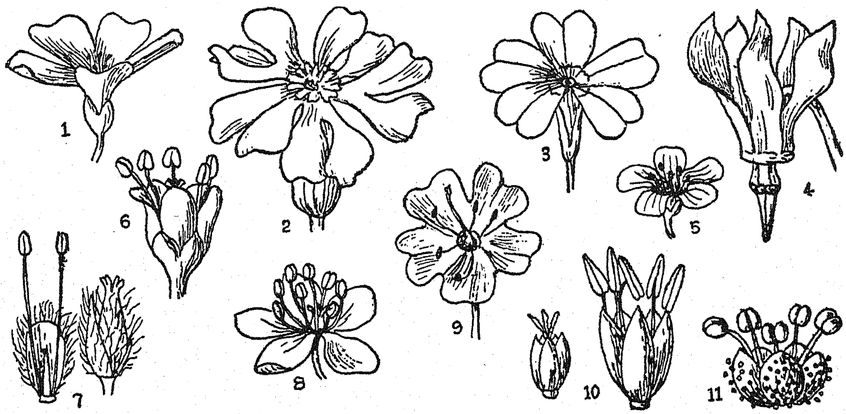

FIG. 10. THE DESCENDANTS OF PINKS
(1) Pink Oxalis; (2) Catchfly; (3) Fairy Primrose; (4) Shooting-star; (5) Spring-beauty; (6) Tamarisk; (7) Alpine Willow; (8) Buckwheat; (9) Four-o'clock; (10) Pigweed; (11) Lambs-quarters

the highest forms, such as the lambs-quarters and saltbushes, division of labor is now at work producing stamen and pistil flowers.

HOW LILIES BECAME PALMS AND GRASSES

While lilies have tried many small experiments in size, color and form of the flower, the family as a whole foreshadows few of the larger ventures in specialization. The calyx early gave up its own task of food-making to aid the corolla in the work of attraction, but the resulting flower has undergone almost no

essential changes within the lilies themselves. In a few cases a number plan of 2 or 4 replaces the usual one of 3, the stamens may be reduced to one row of three, or the three cells of the pistils merged into one. On the other hand, as though to compensate for the lack of enterprise in the flower, the plant-body has exhibited great versatility, especially in the rootstock which takes a variety of forms.

The versatile nature of the plant-body is further revealed in the strikingly different forms shown in the three lines of descent, the palms, rushes and grasses, and the irises. Indeed, the palms are little more than arborescent lilies, and the rushes grass-like ones. Both grow in open places, and this has favored the transformation of the lily flower into one pollinated by the wind. Progress has been somewhat slow in the palms and in some the flower is still essentially that of the tree-like lilies, the dracænas or palm-lilies. In the more highly specialized, the stamens and pistils have been separated and the pistil is reduced to a single cell with one seed, as in the date-palm.

The flowers of rushes would be almost indistinguishable from those of such lilies as the asparagus were it not for the tell-tale evidence of filaments and stigmas, which show the influence of the wind. The latter has also had its effect upon the floral leaves which are dry and rigid in texture, the calyx and corolla being alike in this respect. This fact is significant in the advancing response to wind-pollination, since both dwindle at the same rate and occur in the sedges only as so many bristles. The materials saved in consequence have evidently been utilized in longer filaments and stigmas to insure the transfer of more pollen. This conversion of the protective parts appears to have been overdone, however, for the sedge flower has called to its aid one of the tiny upper leaves to enclose the stamens and the pistil. These advances are accompanied by the reduction of the stamens from six to three and the change of the pistil into one with a single cell and seed. Division of labor also steps in, with the result that in some the stamens are restricted to one flower and the pistils to another, occasionally on different plants. The grasses are direct descendants of the sedges, in which stamens

and pistils are still better adjusted to wind-pollination and two scales are employed to protect the flower and two more the flower cluster, as anyone may easily discover for himself during the open season for "corn-on-the-cob." The effectiveness of all these changes is to be measured by the immense success that the grasses and grains have achieved in nature and under cultivation, and is attested by the fact that man depends upon them for his own food supply, direct and indirect, more than upon all other plants combined. It is not for economic reasons alone that maize is entitled to the name, "King Corn," for it is likewise the most specialized and hence the highest of all plants.

How Lilies Became Irises and Orchids

Descent from the lilies in the insect-pollinated line is so direct as to leave no doubt of close relationship. The changes have been few and gradual, operating in many cases upon some of our largest and most beautiful flowers. The amaryllis, with its nearest of kin, the daffodil, jonquil, snowdrop and tuberose, is bound to the lilies by the most evident ties of consanguinity. Its experience has brought about one striking advance, and this is the placing of the corolla-like perianth on top of the ovary where it will be more readily seen by questing insects. So decisive was this improvement that it has been retained by all its descendants, irises, cannas, bananas, orchids, and others. The iris, with its kith and kin, the crocus, gladiolus, "blue-eyed grass," etc., is little more than an amaryllis in which advancing efficiency in pollination has enabled it to dispense with one row of three stamens. A tendency for the flower to become irregular appears frequently in these groups, only to attain its fullest expression in the orchids. This is felt little or not at all by the three outer parts corresponding to the sepals, but the inner ones have undergone a striking division of labor. This has operated especially upon the lower petal, which has been enlarged to make a huge lip or sack, as in the lady-slipper. This has carried with it the usual consequence of reducing the stamens, first to two, and then regularly to a single one. However, through some curious oversight, the much more significant reduction of the pistil to a single

FIG. 11. THE DESCENDANTS OF LILIES
(1) Alstroemeria; (2) Crocus; (3) Gladiolus; (4) Jonquil; (5) Grass-iris; (6) Rainbow Iris; (7) Yellow Lady-slipper; (8) Snowdrop; (9) Canna

cell with one seed has not taken place. On the contrary, the orchids are the most prolific of all flowering plants, some pods producing more than a million seeds. These are so minute and contain so little stored food that they have practically lost the power of germinating to produce new plants. As a result, the orchids furnish the most striking object-lesson as to the disadvantages to be met in the quantity production of living things.

Roses and Their Kin

Progress among the roses has taken place in two main directions from the simplest forbears, such as the cinq-foil and the strawberry. In the one case, the improvements have been made chiefly in the corolla, producing such unique and beautiful flowers as the sweet-pea, while in the other the advance has been less spectacular but none the less real, yielding the more usual blossoms of the mock-orange and hydrangea. It is a tax upon one's credulity to be told that peas and roses are not only related, but that they actually belong to the same order, and only a scrutiny of the evidence can prove convincing. However, the simplest members of the pea family, the acacias, not only have regular flowers, but these also contain many stamens, as in the roses. The pistil is one instead of many, but the ancestral habit persists to the extent that two or more do sometimes occur. Finally, when one discovers that the butterfly shape of the pea flower has come about through the gradual modifications found in cassia, bird-of-paradise-flower, and red-bud, the puzzle of relationship is solved.

The meadow-sweets or spiræas have improved upon the simple roses by reducing the pistils to five, more or less sunken in a cup that bears the sepals on its margin and the petals and stamens on these, just as in the rose. The red-haw, apple and pear have sprung from the meadow-sweets by making the cup fleshy and bright-colored to attract animals to do the work of seed-distribution and by fusing it with the papery pistils that form the "core" of the apple. The advantage derived from raising the petals is reflected in the decrease of the pistils to one in the peach, apricot, cherry, plum and almond, the wall becom-

ing fleshy or fibrous on the outside and stony within, forming a "pit" that protects the seed against digestion. In the competition between the two seeds, usually but one develops, though a "philopena" is an almond in which both seeds have matured.

How Roses Became Cacti

The mock-oranges are probably direct descendants of the spiræas, marked by the further advance in which the pistils

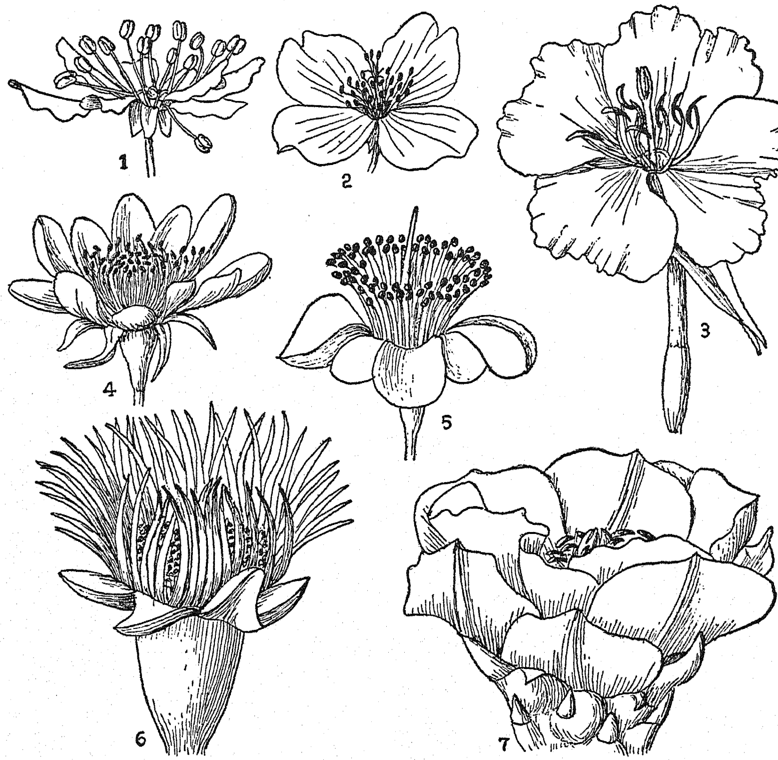

Fig. 12. The Ancestry of the Cactus
(1) Spiræa; (2) Mock-orange; (3) Yellow Evening-primrose; (4) Evening-star; (5) Myrtle; (6) Noon-flower; (7) Yellow Prickly-pear

are united to form a compound one. This is accompanied by the elevation of the corolla, which together with the numerous stamens furnishes the distinguishing feature of the line of

descent that terminates in the cacti. There is practically no break in this line as it springs from roses, the mock-orange approaching the common myrtle so closely that they seem to be first cousins. The myrtle family is an enormous one in the tropics, including eucalypts, clove, allspice, and guava, and serving as the parent stock for fireweeds or evening-primroses on the one hand and cacti on the other. The efficiency of the former is indicated by the reduction of the stamens to two rows of four each, this family being especially set apart by its number plan of 4.

In the other direction, the stamens remain numerous and the number of pistils large as a rule through the meadow-beauties and the noon-flowers, and these pass into the evening-stars and cacti, which incline to economy, as shown by the removal of the partitions in the ovary. The noon-flowers or ice-plants, and cacti are alike in having fleshy plant-bodies, but it is the leaves that are succulent in the one and the leafless joints of the stem in the other, though a few cacti still possess leaves. In the popular mind, nearly all spiny plants are confused under the name of "cactus," but this term belongs properly only to those plants with the peculiar flower of this family. The noon-flowers and cacti are also alike in having a large number of petals and stamens, a feature probably associated with the storage of water in the fleshy parts and the consequent assurance of a permanent supply of raw material.

How the Roses Became Maples and Walnuts

The woody habit so common in the rose family carries with it a number of advantages, the chief of which is that the plant-body does not need to be reconstructed anew each year, but can begin growth where it left off the preceding autumn. On account of their stature, trees are peculiarly fitted to employ wind for the transfer of pollen. Moreover, when the flowers are small and more or less hidden by the mass of foliage, insects save themselves trouble by neglecting them, with the consequence that a premium is placed upon wind-pollination. The result of all this is that the line of descent leading to the oaks and walnuts

has been more and more controlled by this process. The corolla disappears and the flowers become smaller and more inconspicuous, thus giving warrant to the popular belief that our common shade-trees and nut-trees do not bear flowers.

The hydrangeas differ from the mock-orange in no important respect, and they might well belong to the same family. From them it is but a short step to the witch-hazels, and thence to the sumacs and bitter-sweets. The corolla is still present in most of these and is often accompanied by nectar, but the flowers are usually small and neutral in color. The flowers of the simplest maples are very similar, but most species have lost the corolla and division of labor is actively converting perfect flowers into staminate and pistillate ones. In the maple that we call box-elder, the goal of specialization has been reached, and the two kinds of flowers are found on separate trees. In the birches and alders, these flowers are grouped in catkins—suggestive of pussy willows—and the staminate ones hold this habit throughout. The increasing parental care given the pistillate flower has brought about the disappearance of this catkin and permitted the specialization of the fruit, seen in the beechnut, the acorn, the chestnut-bur and the walnut.

How Roses Became Sunflowers and Dandelions

The main line of descent from the roses seems likewise to have sprung from the witch-hazels. These pass almost imperceptibly into the dogwoods, marked by a single row of stamens instead of two, and the latter are regarded as the direct ancestors of the parsleys or umbellifers with their umbrella-like clusters of flowers. A much more important advance was the fusion of the petals by which the dogwoods gave rise to the honeysuckles and madders, perhaps through the elderberry, which is little more than a dogwood with united petals. The experience of the true honeysuckles has been such as to bring about the production of an irregular corolla with two lips. However, the main line of descent passes through the closely related madders, which have regular flowers and are hence considered to be the ancestors of teasels, bluebells, and asters.

The ancestral history of the asters can be traced only after it is realized that the sunflower, aster, chrysanthemum and dandelion are not at all single flowers but dense clusters of tiny florets, a fact from which they take the name of composites. If a floret is pulled from the disk of a gaillardia, it is found to

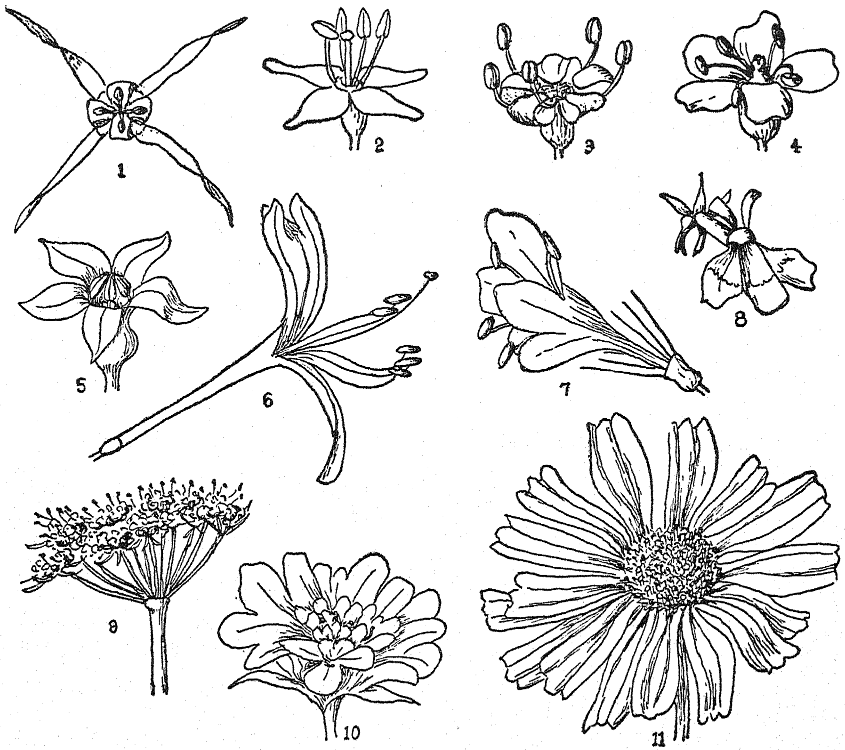

FIG. 13. THE ANCESTRY OF THE SUNFLOWERS
(1) Witch-hazel; (2) Dogwood; (3) Fennel; (4) Elderberry; (5) Madder; (6) Honeysuckle; (7) Scabiosa, Ray-flower; (8) Lobelia; (9) Mountain-parsley; (10) Scabiosa, Head; (11) Bush-sunflower

have a tube-like corolla and a papery calyx on top of the ovary, with a ring of stamens inside and a forked style, reminiscent of the two cells in the ancestral pistil. Similar flowers are found in the madders and bluebells, as well as in teasels and valerians, all of which are relatives of the composites. These plants have

discovered that co-operation is the best solution of many of their problems, a secret that they have passed on to the composites, which have applied it most thoroughly and with striking success. Earlier experiments in co-operation were not unknown, as the clovers testify, but these were incidental and did not lead to the general adoption of the principle. Flowers of considerable size proved sufficiently attractive when single or in small groups, and it was not until the small size of parsley flowers led this family to develop the umbel that the values of orderly massing were revealed. Once discovered, co-operation was appealed to more and more, until in the asters it came to be the universal method of securing greater efficiency.

Co-operative Flowers

The advantages of massing are nicely illustrated by the hydrangea, in which the huge cluster not only increases the visibility many times, but also offers an opportunity for a co-operative division of labor by which the outer flowers are devoted to attraction and the inner to seed-production. In the blue lace-flower of the garden, this tendency is emphasized and the outer flowers of the umbel serve for landing as well as attraction. The calyx of the individual flowers is too much reduced to carry on the usual tasks of food-making and protection. Moreover, these can now be done better on the co-operative plan for the cluster as a whole by grouping ordinary leaves just below it. This new structure is really a sort of compound calyx, but since the flowers are rolled up in it in the bud, it is called an involucre. However, the calyx is not placed on the retired list, but is assigned a new job. In the valerian it grows out into plumes that float the seed-like fruits away on the wind, and in forms still more perfected it furnishes aerial transport for the vast majority of the asters, the dandelion being the flying ace among composites.

Co-operation in attraction is the most conspicuous feature of the composites. In addition to the massing of the florets in heads, the chief rôle in attracting insects has been assigned to the marginal flowers, which have turned into long bright ribbons,

best seen in the heads of single sunflowers, dahlias and chrysanthemums. In the flowers of the thistle, boneset, ironweed and others, these ray-florets are lost, while in the dandelion, chicory and goats-beard they are multiplied to give the effect of a "double" flower. In short, the head as a co-operative community devoted to attraction and seed-production has repeated in its essential features the experience of the single flower in solving its problems by specialization. It affords outstanding evidence of the many advantages of co-operation, division of labor, conservation of energy and material, and increased parental care, and furnishes many an object-lesson for man in his great task of converting human communities into effective co-operative units.

THE WORK OF FLOWERS

The Day's Work

VIOLETS on a shady bank or buttercups in a sunny meadow wear an air of placid contentment apparently far removed from thoughts of work or problems to be solved. Yet each flower is going through its daily round of duties, from the time the bud bursts until the fruit is ripe and the seeds scattered. This is at once discovered by returning to the same flower morning, noon and night, or from one day to another, though a close scrutiny is often required to disclose what the smaller

Fig. 14. Flowers That Never Close
(1) Pansy; (2) Leopard Lily; (3) Wild Rose

parts are doing. In some plants the whole flower suddenly opens and then closes, or the fruit abruptly flies apart and starts the seeds on their journeys. In others, the leaves may close at a touch, or they fold their leaflets in sleep at night and expand them in the morning.

It is soon realized that plants are not mere living things passively absorbing the sunshine, but active workers carrying out the usual daily tasks and meeting new situations as they arise. While they seem much less alive than animals, this is largely because they are rooted to one spot and their activities escape the eye more easily. It is the ceaseless industry of green

plants that provides the food-supply of the entire world, primarily for the plants themselves, but eventually likewise for all animals, including man. To accomplish this, they must work on a 24-hour shift, though the labor is divided in such a way that more is done in the sunshine. Many of their flowers have an equally long day too, the rose, lily and pansy staying open day and night for days and even weeks. The tulip, gentian

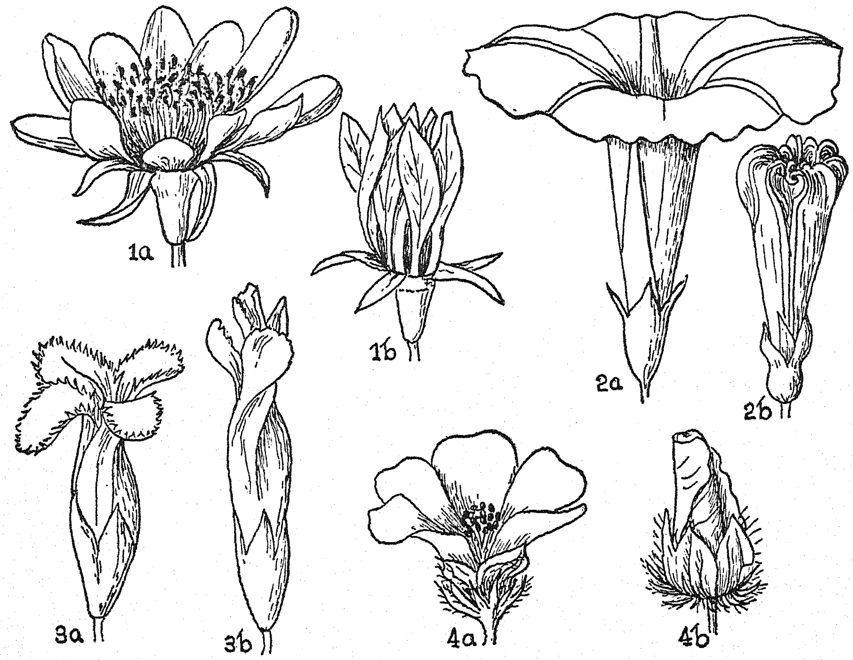

FIG. 15. FLOWERS THAT OPEN AND CLOSE
(1) Evening-star; (2) Morning-glory; (3) Fringed Gentian; (4) Flower-of-an-hour

and dandelion belong to the day shift, beginning work in the morning sunshine and stopping in the afternoon, while the four-o'clock, evening-star and moon-vine open as the sun sinks and close as it mounts again. The active work of the morning glory and spider-wort is finished before noon, and the flower-of-an-hour hurries through its tasks in the shortest time of all.

ATTRACTION

It would seem that our Aryan forefathers had at least an inkling that flowers work, since both "flower" and "bloom" are merely different forms of the same word, meaning "that which blows or opens." At a later time when the parts of the flower were given their names, these came also to suggest something of the work of each. The bright-colored circle of leaves draws the eye at once and this readily explains why it was called the "corolla" or crown of the flower. It is the corolla that constitutes the charm of our favorite flowers of field and garden and gives to each its own peculiar personality. Its chief task is to attract insects as well as humming-birds for transfering

Fig. 16. Types of Double Flowers
(1) Prickly-pear; (2) Stock; (3) Marigold

pollen from one flower to another, and the success of each flower may be measured by the skill with which it does this. Flowers have many ways of increasing their attractiveness, but many of them make use of "doubling," or of coloring some other part. In such blossoms as those of the pond-lily and the night-flowering cereus, the attraction of the corolla is enhanced by several rows of leaves or "petals." Such doubling occurs only here and there in nature, but it is promoted by cultivation and there is almost no limit to the number of double flowers that the skill of the florist can produce. The improvement of the dahlia and chrysanthemum has gone so far that it is almost impossible to realize that the marvelous blossoms of the flower-show were once "single" heads like those of the sunflower and daisy.

A somewhat similar change in the attractiveness of the corolla has been secured by transforming the green leaves of the calyx into brightly colored ones. In the lily and the iris this change is so complete that the flower seems to be all corolla, until one looks closely and discovers that three of the supposed petals differ in their markings and position. In addition to resembling the lily in this respect, the daffodil and jonquil owe much of their striking beauty to a colored cup or crown inside the corolla. The calla "lily" rolls a large white leaf into a cornucopia around the central stem of tiny yellow flowers and hence is not a lily

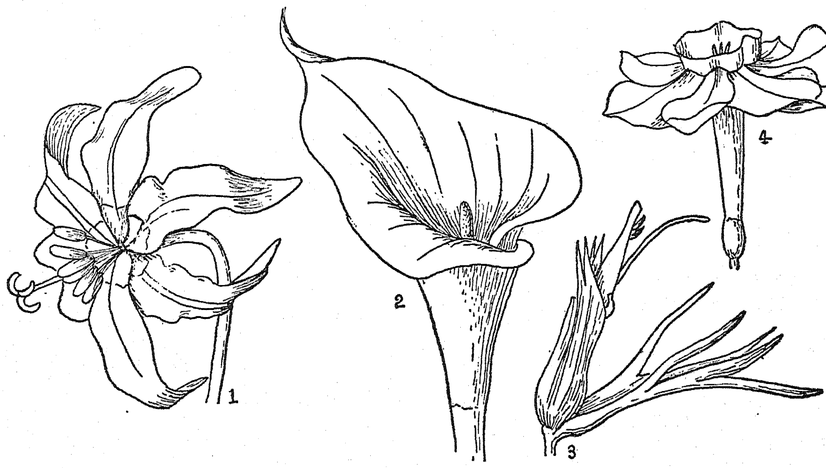

Fig. 17. Accessory Devices for Attraction
(1) Spring-lily; (2) Calla; (3) Scarlet Paintbrush; (4) Jonquil

at all, but a close relative of the jack-in-the-pulpit, which streaks its leaf with green and yellow. The brilliant hues of the paint-brush are due but little to the flowers themselves, which are half concealed by the vivid leaves or bracts beside them.

The color of the corolla brings the insect to the flower, but once arrived, it must be guided to the store of sweets in the nectary. This task is slighted by the buttercup and other flowers in which the petals are all alike and uniform in color, but more attention is paid to it by the geranium and similar flowers with stripes converging toward the nectary. Much more skillful guid-

ance is afforded by the so-called irregular flowers, which have petals of two or more shapes or sizes. The lower petal of the violet is enlarged or lengthened to serve as a landing platform, and is often striped and grooved for further guidance. In the snapdragons and the sages, the landing platform is made of three petals united to form the lower lip of the flower, while the tube within is often fashioned or marked for guidance. The most complete specialization for effective work is found in the sweet-pea and its relatives, where one petal is greatly enlarged to form the standard, two make the wings and the other two are united into the keel. The standard acts both as an attractive banner and a landing place, the wings serve for support, and the keel encloses and protects the delicate stamens and pistils.

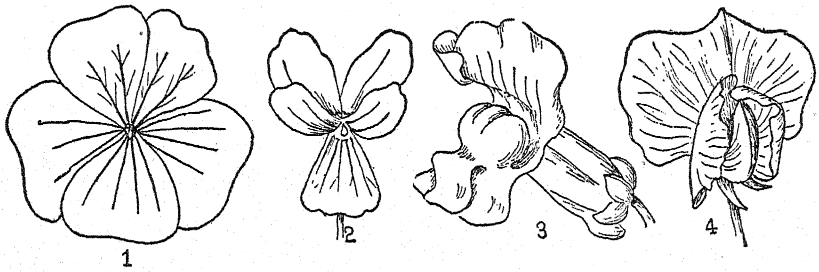

FIG. 18. GUIDE-LINES AND GROOVES
(1) Geranium; (2) Wild Pansy; (3) Snapdragon; (4) Sweet-pea

Once found in the blossom, the nectar itself is a powerful inducement for the visitor to return. As a consequence, the most successful flowers produce a large amount of nectar, and many of them have modified the corolla to store or protect it from rain or from marauders. Some flowers exude nectar from the base of the petals and it collects at the bottom of the flower in drops or as a film. In the violet and the bleeding-heart, it is stored in a special sack, while in the columbine the nectary takes the form of a long spur on each of the petals. Diluted nectar soon loses its charm and wet pollen is difficult to carry, with the result that many flowers employ the corolla to protect these from both the rain and the dew. In the hanging flowers

of the bluebell and many heaths, the shape and position of the corolla afford almost complete protection, while in the crocus, tulip and fringed gentian this is secured by closing the corolla at night or before a rain. In some flowers that seem directly exposed, like the phloxes and puccoons, the mouth of the corolla is often so small that rain-drops can not enter, or the opening may be closed by hairs. The best protection is afforded by those

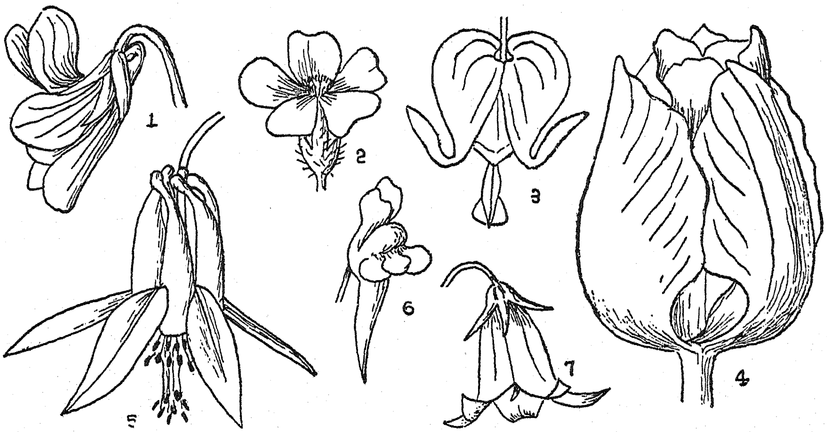

FIG. 19. DEVICES FOR STORING AND PROTECTING NECTAR
(1) Prairie Violet; (2) Anchusa; (3) Bleeding-heart; (4) Tulip; (5) Red Columbine; (6) Butter-and-eggs; (7) Bluebell

corollas that open little or not at all, except under pressure, as is the case in sweet-peas, butter-and-eggs and skull-caps.

PROTECTION

The circle of green leaves below the corolla is called the "calyx," from its function of covering and protecting the other parts in the bud. It is usually green in color and hence resembles an ordinary leaf in its work more than it does its brilliant associate, the corolla. This is best seen in flowers with a large calyx, such as the peony and hollyhock, and is further suggested by the hepatica and wind-flower in which the calyx has lost its green color and food-making habit and this work has been assumed by the circle of calyx-like leaves. Because of their

close association, it is not strange that the calyx should often imitate the corolla and exchange its coat of dull green for one of brighter hues. The imitation is often so close that the sepals of the calyx can be distinguished from the petals only by their position, as in many flowers of the lily and amaryllis families. The larkspur and monkshood have not only colored the sepals, but have also changed their shape to form an irregular flower that seems to be all corolla. The illusion is all the greater from the fact that a spur or hood has developed to hold or protect

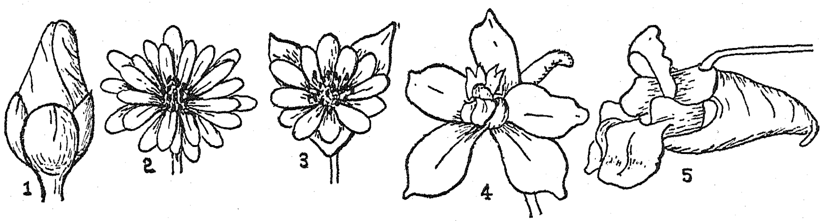

FIG. 20. SPECIAL FORMS OF THE CALYX
(1) St. Johnswort; (2) Windflower; (3) Hepatica; (4) Larkspur; (5) Touch-me-not

the nectar, a change to be found likewise in the touch-me-not and the nasturtium of the garden.

PRODUCTION OF POLLEN AND SEEDS

The special duty of the stamen is to produce pollen, and shed it in the manner most favorable to transport. The pollen is borne in the yellow sack at the tip, which is called the anther, and this is usually supported on a thread-like stalk, the filament. The dust-like pollen is sifted out through a narrow slit or pore in the anther in such a way as to increase its chances for successful transport. In a few flowers the anther bursts forcibly and showers the visiting bee with the whole load of pollen. The filament takes care of the work of placing the anther in the best position for the removal of pollen, and its growth or movement is a significant feature of both cross- and self-pollination in insect flowers. In the wind-pollinated flowers of box-elder, plantain, and most grasses, the long filaments hang the anthers out in such fashion that the slightest breeze may carry the pollen

away. The most efficient filaments are found in the scarlet sage, where they are modified to form a trip by which the bee applies the powdery anthers to his own back. When the anthers of a flower are numerous, they play a part in attraction, since the abundant pollen is eagerly sought for "bee-bread" to feed to the young. Occasionally they are red, blue or green and then have some attractive value, as the filaments may also have when they are vivid and numerous or united into a column, as in the hollyhock and the cardinal-flower.

The pistil performs the most important work of all the flower parts by developing and caring for the young plants or seeds. These are contained in the swollen base, or ovary, which protects and nourishes them as well, as may be inferred from its green color. The important task of catching the pollen-grains and enabling them to germinate is assigned to the stigma, a sticky disk usually placed above the ovary on a thin stalk termed the style. This serves to place the stigma in the best position for receiving pollen, just as the filament of the stamen promotes loading it. The form of both stigma and style depends upon the agent that transports the pollen and consequently differs greatly in insect and wind flowers. The work of the stigma ceases when the flower withers, but the ovary is often called upon to develop pulp, hooks or spines for transporting the seeds to a distance and in rare cases the style is also utilized for this purpose.

The Daily Round in Representative Flowers

While all the efforts of the flower are directed to the making of seeds, the indispensable task of pollination consumes most of its time and energy. Some flowers produce seeds without ever opening, as the woodland violet and the wild touch-me-not, but such cases are rare, and opening, or "blooming," is an all but universal prerequisite. Without it the transfer of pollen from one flower to another is impossible, and in most plants this is indispensable for the best results. Its importance is shown by the industry and skill that flowers exhibit in bringing about cross pollination and has been confirmed by the experiments of Darwin, who found that such a transfer insured the production

of more and better seeds. The story of each flower is the record of the changes it undergoes to insure cross-pollination or to resort to self-pollination when this fails, and of the development of fruit and seed in consequence. The tasks of the flower and the activities of the pollinating insects are necessarily carried on at the same time, but a clearer picture may be obtained of each if it is followed through by itself. The detailed steps taken by one kind of flower are often so many and so different from those of another that it is helpful to realize that all of them fall into a few stages. These are opening, cross-pollination, self-pollination when necessary, setting the fruit and scattering the seeds.

GERANIUM

A morning visit to the wild geranium as it is coming into bloom leads to the discovery that the buds change position as

FIG. 21. THE DAILY ROUND OF THE GERANIUM

they start to open. The young buds hang directly downward for several days before they move slowly upward, as they increase in size. On a warm sunny morning the oldest bud in each cluster will begin to rise and it reaches the horizontal position in 12 to 24 hours. Usually at this time the tips of the calyx separate and the pink corolla peeps out. By sunrise the bud is erect, the corolla is swollen and the petals are loosening at the edges; they soon separate, forming a pink cup in the center of which lie the plump anthers. By evening or early the next morning,

the filaments have swung the anthers out in two distinct rows, and those of the outer row crack open and begin to shed their pollen. Several hours later, or as much as a day after when the weather is cool, the pollen is mostly gone and the inner row starts to shed. The next morning the pollen has vanished, the anthers begin to dry and darken, and the filaments again bend inward. The anthers continue to drop and the column of stigmas opens from the tip downward, until the five stigmas are revealed. These move to a horizontal position, where their bristly surfaces are ready to receive pollen from another flower and the tips then twist spirally. This stage persists for a day or two, after which the petals wither and drop from time to time, while the stigmas begin to dry.

The sepals then slowly rise to a nearly erect position about the stigmas and filaments, and the ovary beings to swell with the forming seeds. The growth of the pistil into the mature fruit requires two or three weeks, its cranesbill form becoming more and more marked. It ripens gradually to the point where the tension of the styles causes them to curve outward at the base and throw the seeds some distance from the parent plant.

LARKSPUR

In spite of its more specialized corolla, the work of the larkspur is really simpler than that of the geranium and consists largely of ripening the anthers at a fairly uniform rate to maintain a constant supply of pollen for attraction and transfer. The blue calyx first opens in the course of a day or two and the petal tips separate, disclosing the many stamens, which are turned downward. Soon after, two or four of the uppermost stamens turn upward and the anthers crack open. After several hours their pollen is largely gone, and the anthers move upward and out of the way as they shrivel. Under the usual conditions new groups of anthers exhibit these changes at intervals of 6 to 12 hours, until all have shed. Toward the end the stigmas appear in the midst of the empty anthers and are soon ready to receive pollen brought from other flowers. After pollination they begin to swell visibly and at the same time the anthers dry up and

fall, and the sepals and petals begin to drop. In two or three days all that remains of the flower is the fruit, consisting of three spreading horn-like pods. These ripen in a few weeks,

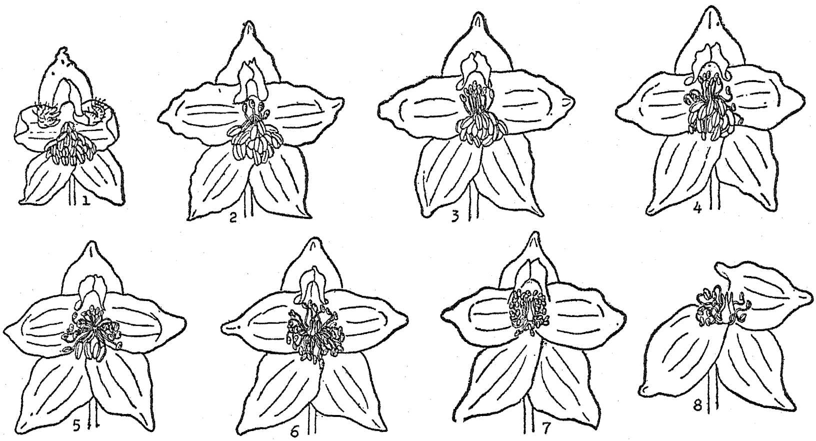

Fig. 22. The Daily Round of the Blue Larkspur

split along one side and allow the seeds to fall to the ground about the parent plant.

HERACLE

When the stamens are only four or five, the need for a continuous supply of pollen demands that they act independently of each other rather than by circles or groups. This is the behavior in the tiny flowers of the parsley family, and is best shown in the heracle or cow-parsnip. The infolded petals split along their edges shortly after sunrise, revealing the stamens tucked away in the gaps. The flower swells rapidly and one filament slowly straightens up above the incurved petals. This anther usually cracks before noon as the filament bends outward and the second stamen takes a similar position. Meanwhile the petals have spread more and more widely, uncovering the three incurved stamens. By the following morning the second anther is shedding its pollen and the third is carried up to the same position, after which it also cracks and frees the pollen. The other two stamens follow in their turn at intervals of a few hours and by the morning of the third day most of the pollen has been shed and the

petals are widely spreading. Shortly afterward the filaments start to bend down, usually one or two at a time and by the next day the shrunken anthers are carried well below the petals.

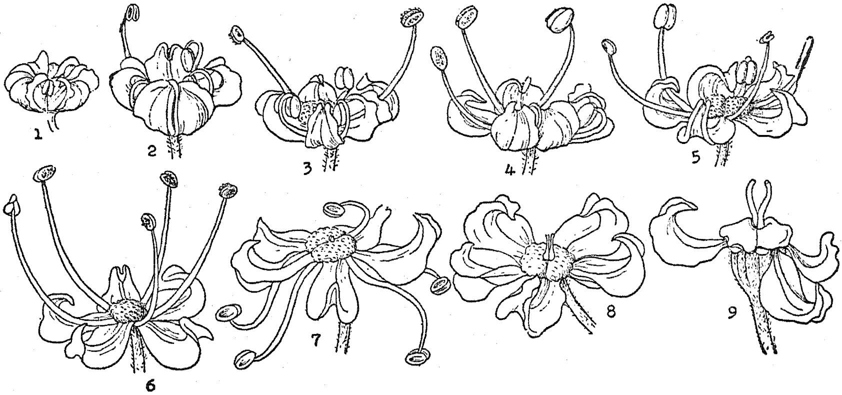

FIG. 23. THE DAILY ROUND OF THE HERACLE

At the same time the two stigmas appear in the middle of the sticky disk and are ready to be dusted with pollen. The stamens fall away as the stigmas enlarge and are soon followed by the withering petals, the flower finally changing to a short pod capped by an enlarged disk with the stigmas curving and drying.

BLUEBELL

Although the bluebell also has but five stamens, it carries on its work in an entirely different manner, owing to its making a special device for conserving pollen. The young buds are erect at first and gradually bend over as they become larger, first becoming horizontal and then hanging downward. At this time the anthers are joined in a column about the style, and they start to burst and free the pollen before the corolla opens. This continues as the mouth of the corolla widens, the shrunken anthers coiling about the base of the style and leaving the brush above coated with pollen. Shortly afterward the three stigmas begin to separate at the tip, while the dry anthers untwist and contract into the bottom of the corolla. The stigmas spread more widely, curving backward and exposing the sticky surfaces for

the deposit of foreign pollen, often for a period of several days. Finally, the corolla wilts and then collapses into a wrinkled bag with the stigmas still projecting from the top. The bag

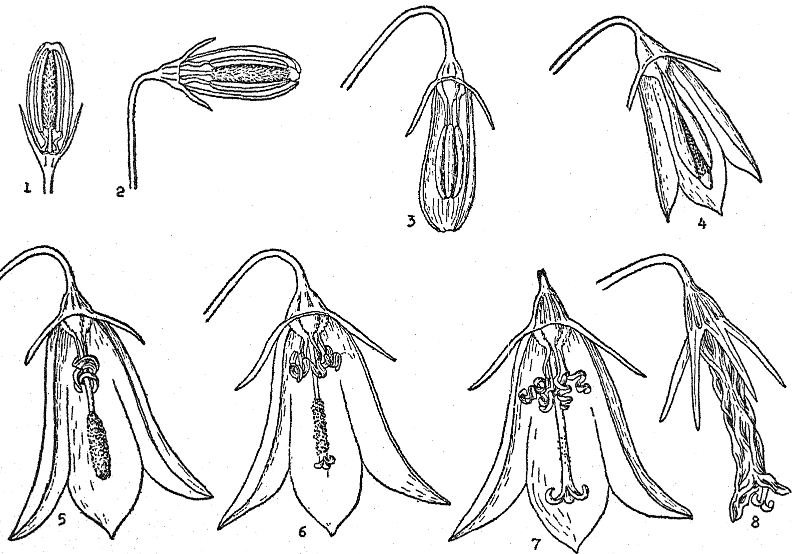

FIG. 24. THE DAILY ROUND OF THE BLUEBELL

dries up and falls off as the pod enlarges. After a few weeks the pod ripens, makes five little openings on the sides and the seeds are sifted out as it is shaken back and forth by the wind.

PAINTBRUSH

On account of its curious shape, as well as the fact that the corolla is hidden for some time by the colored bracts and calyx, most of the work done by the flowers of the paintbrush escapes attention. The stigma first peeps out of the small hole at the tip of the closed corolla when the latter is entirely hidden in the calyx. It then turns forward and is pushed out through a slit as the corolla grows upward. As the latter lengthens, it appears at the top of the calyx with the style projecting from it. At this time the four anthers burst in unison and the pollen is packed in a dense mass in the upper half of the corolla. This unusual behavior is made possible by the fact that the corolla is so nearly closed that the pollen can neither he shaken out by

the wind nor stolen by robber insects. The corolla finally grows a half-inch or more beyond the calyx, still tipped by the receptive stigma. The latter soon wilts and curves downward and

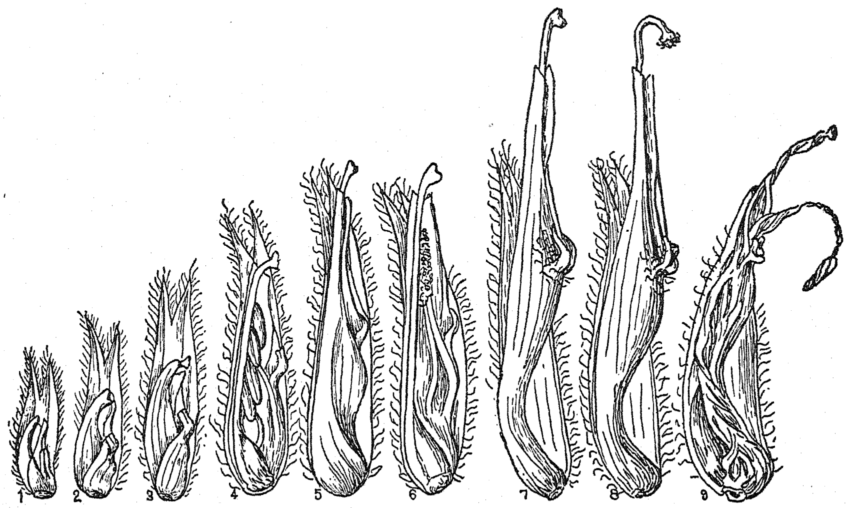

FIG. 25. THE DAILY ROUND OF THE PAINTBRUSH

in a day or so the two lips of the corolla shrivel and the whole collapses into a wrinkled bag with loose ends.

MORNING GLORY

The flower buds of the morning glory require three or four days for their development. The first day the green tip of the corolla appears between the calyx lobes and the second day it lengthens to a half-inch or less. It continues to lengthen and grows pinklish on the third, and is fully open on the morning of the fourth day. However, if one follows the swollen buds carefully through the day, it will be seen that the name "morning glory" is somewhat misleading. The spiral of the bud begins to uncurl at the tip between one and two in the afternoon, leaving a small opening which widens slowly until sundown when it is a quarter of an inch across. The change then proceeds more rapidly and between eleven and twelve o'clock the flower becomes fully expanded. It greets the dawn in this condition and even to the early riser appears to have just unfolded.

The stigma lies above the opening anthers through most of the morning, and cross-pollination is effected by butterflies and humming birds especially. On warm days in the sun the corollas begin to show signs of wilting at the edge and by the middle of the afternoon the spreading portion has collapsed into a ring.

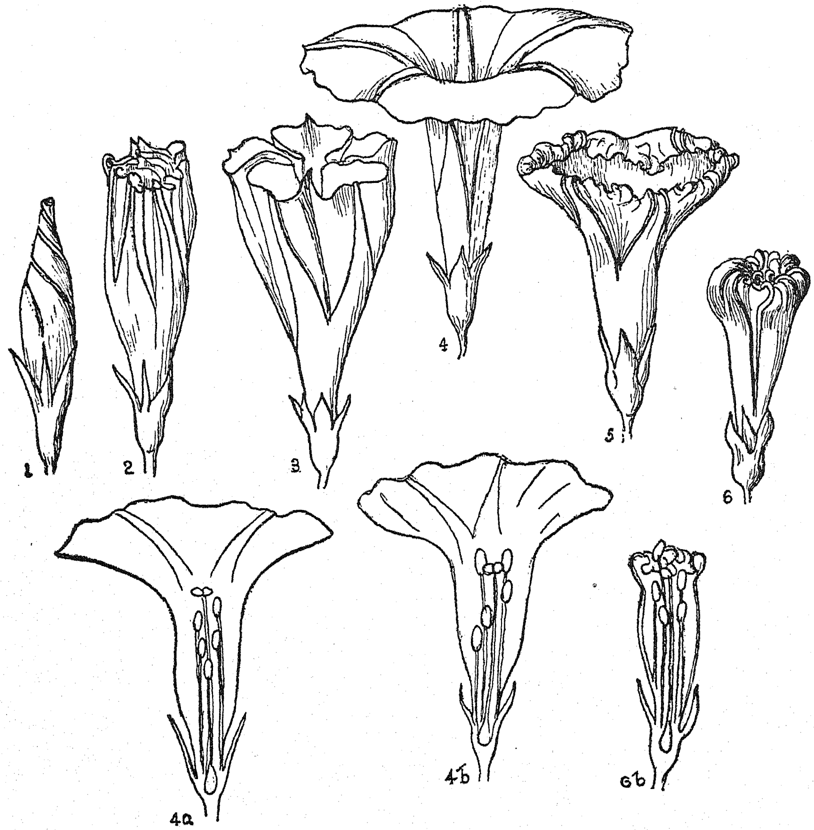

Fig. 26. The Daily Round of the Morning Glory

In the shade the corolla may last all day, and on foggy days this is a frequent occurrence. During the wilting of the flower one or more of the filaments have elongated, carrying the anthers above the stigma. As the corolla shrivels and dries the second morning, pollen may be transferred to the stigmas, and self-pollination may ensue if cross-pollination has not already taken

place. The dried corolla persists for a day or two and then falls, disclosing the young fruit.

Standardized Methods in Pollination

INSECT POLLINATION

The energy that the flower devotes to securing pollination is readily explained by the fact that pollen is indispensable to the

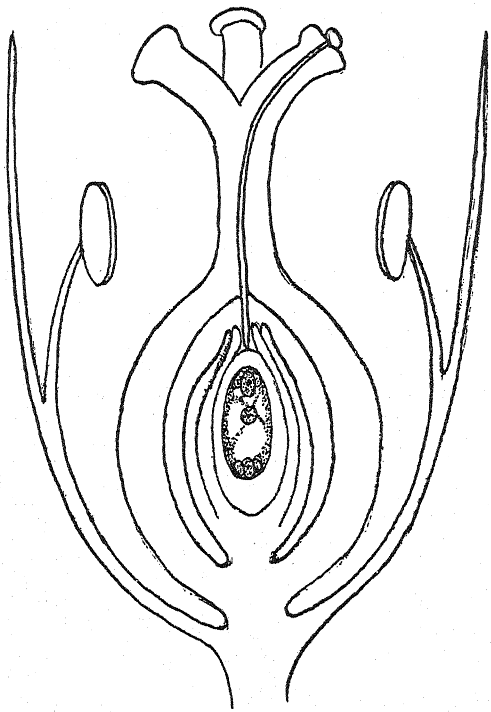

FIG. 27. DIAGRAM OF THE KNOTWEED FLOWER SHOWING FERTILIZATION

production of seeds. The pollen-grain is actually a spore, protected by the thick wall from drying out in its journey from one flower to another. Like the spores of mosses and ferns, it germinates under favorable conditions, which in its case consist of the sugary solution poured out on the stigma of the pistil. This causes the grain to swell and burst the wall, permitting the

pollen-tube to grow down the style into the ovary. Here the tip enters one of the ovules or young seeds, where the tiny sperm escapes and unites with the egg-cell to form the young plant found in each ripe seed. This is the crucial step in the work of the flower, but its accomplishment depends wholly upon the success of the pollination that leads up to it. As a consequence, while the making of good seeds is the supreme purpose of the flower, it expends most of its time and energy on producing, protecting and transferring the pollen, and by far the largest amount of this on the task of transfer.

Since most plants have flowers that contain both stamens and pistils, it seems at first thought not merely unnecessary but even wasteful to work so hard to have the pollen carried away to the pistil of another flower. This appears to be entirely opposed to the principle of conservation of material and energy, which is such a controlling factor in the life of the plant. However, the transfer of pollen from one flower to another is so nearly universal that there must be a compelling reason for it. As already indicated, this reason has been supplied by Darwin, who showed that better seeds and more vigorous offspring resulted from pollen brought from another flower, either of the same or of a different plant. This made it clear why nearly all flowers are so constructed as to favor cross-pollination and many are adapted to this method alone. However, self-pollination, or the transfer of pollen between the anther and stigma of the same flower, is far better than none at all, and the great majority of species have taken much pains to secure it, when for any reason cross-pollination has not succeeded.

One may at first be puzzled to understand how the so-called perfect flower, which has both stamens and pistil, can both prevent and promote self-pollination, when these two organs are crowded together in the same flower. The answer is found in the fact that the pollen is ripened and shed before the stigma is ready to receive it, or more rarely the stigma becomes receptive before the pollen is ready. In neither case can self-pollination occur, even though anther and stigma touch or the pollen fall directly upon the stigma. Usually a period of several days

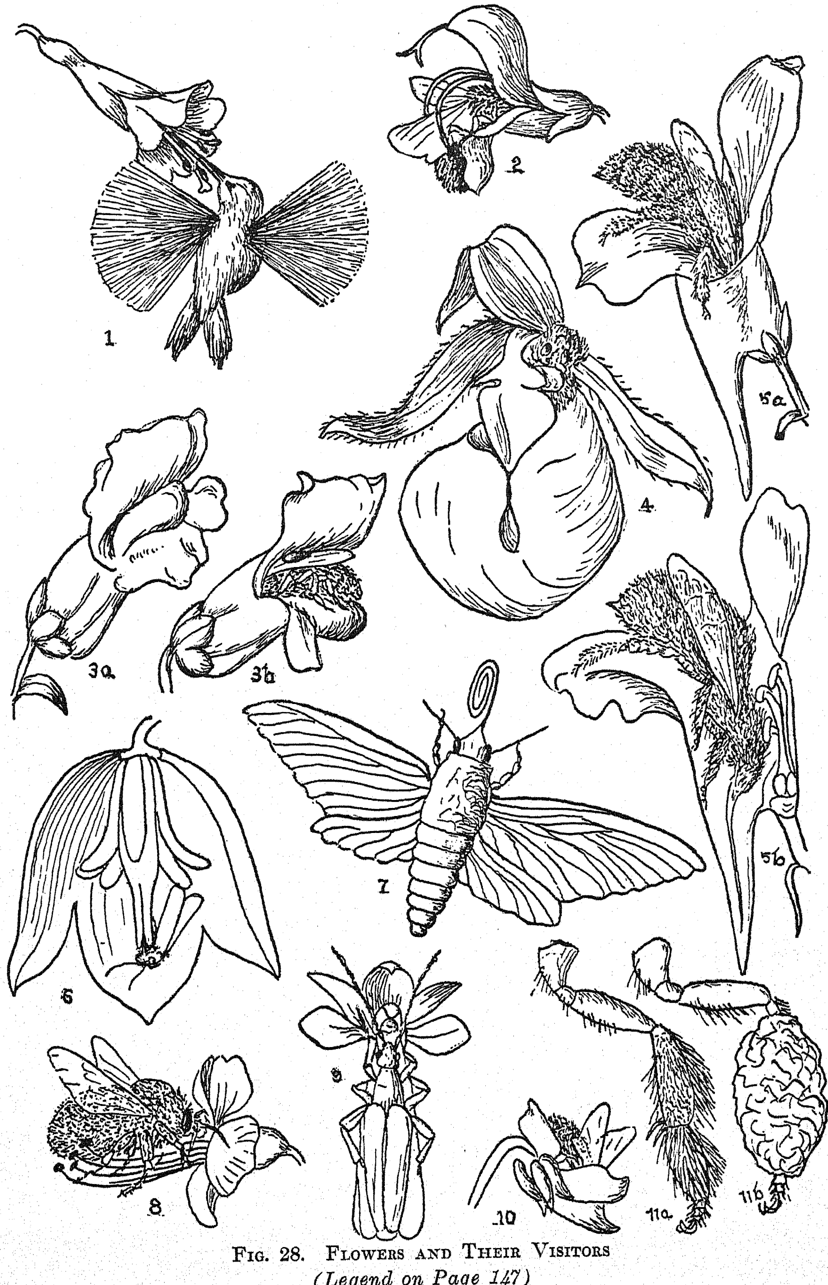

FIG. 28. FLOWERS AND THEIR VISITORS
(Legend on Page 147)

intervenes, during which pollen is carried away to other flowers or brought from them. Finally, as the flower grows old, changes in the position of stamens or style, or the act of closing or wilting may serve to bring the anthers and the stigma together. If cross-pollination has already taken place, this is of no effect, but if it has not, some of the pollen-grains that still cling to the anthers may bring about self-pollination. Cross-pollination is so much the rule that the changes concerned in it are apt to fix the attention to the neglect of those later employed to make self-pollination possible, but these can be discerned in most bright-colored flowers and even in many of the dull ones that are pollinated by the wind.

The thought may readily suggest itself that, since self-pollination is less desirable than cross-pollination, the latter may be more effective in some cases than in others. This actually seems to be true, though the proof is not yet so conclusive. The transfer of pollen to a flower of another plant apparently gives better results than between two blossoms of the same plant. This seems to furnish part of the explanation of the exceptional vigor and success of those species with stamen-bearing flowers on one plant and pistil-bearing ones on another, and something of the same advantage probably arises from separating the stamens and pistils in the flowers of the same plant.

The presence of bright color in a blossom is an almost universal sign of pollen transport by insects or birds. The absence of a vivid corolla or calyx is less decisive, though the vast majority of small green flowers depend upon the wind for pollination. The catkins of the pussy willows and their relatives furnish an exception, owing to the fact that they contain nectar and hence are visited by swarms of bees. The blue woodland violet is an exception to both statements, inasmuch as the bright blue blossoms produce neither pollen nor seeds, while this work has been assumed by tiny bud-like flowers that are self-pollinated without opening. The curious form and brilliant colors of the sweet-pea make it clear that this is designed for insect pollination, but it is regularly self-fertilized, since only the strongest bees can force the petals open and reach the nectar. While both

closed and vivid self-pollinated flowers are of special interest, they are relatively rare, and the story of pollination centers about transport by bees and by the wind. It is usual to speak of the two kinds as insect-pollinated and wind-pollinated, but it seems entirely proper to refer to them briefly as insect flowers or wind flowers. For the sake of furnishing the flower-lover with a simple yet adequate introduction to the co-operative work of insects and flowers, the life-history and the insect behavior are given for a number of representative types, among which are included several wind flowers.[1]

FIREWEED

The fireweed is an admirable flower for following the work done in the course of pollination, owing to the exceptional number of movements it exhibits and its remarkable success in attracting visitors. When blossoming is ready to begin, the buds are all hanging down in a slender cluster a foot or two long. Those at the bottom start to rise, swinging slowly upward on the short stalk until they become horizontal. Soon after, the petals loosen at the tip and curve backward until they are more or less vertical. At this stage the four longer stamens are directed forward, the four shorter hang downward, and the style is turned sharply back out of the way. Two of the upper anthers begin to shed their pollen after three or four hours and are soon followed by the other two. By the next morning some or all of the lower anthers have moved forward and begun to shed, and the style has swung more or less directly downward. The four stigmas now begin to separate and are soon carried by the style into the position formerly occupied by the anthers, which have shrunken down and back out of the way. The lobes are coiled and ready to receive the pollen brought from other flowers. The flower remains in this stage for about a day, permitting abundant opportunity for pollination before the petals begin to close, leaving only the stigmas projecting. A day or so later the petals begin to wither, shrinking away from the projecting style and disclosing the dried stamens below. Shortly after, the flower

[1] F. E. Clements and Frances Long. 1923. Experimental pollination.

falls off, leaving the ovary to grow into the pod-like fruit. This gradually turns upward on its stalk until it is upright, after which it ripens, first cracking at the tip into four walls and allowing the plumy seeds to sail forth on the wind.

The fireweed usually grows in dense masses four to ten feet tall and its great clusters of brilliant pink corollas exert a strong attraction for bees especially. This is enhanced by the abundant supply of nectar at the base of the petals and to a small degree

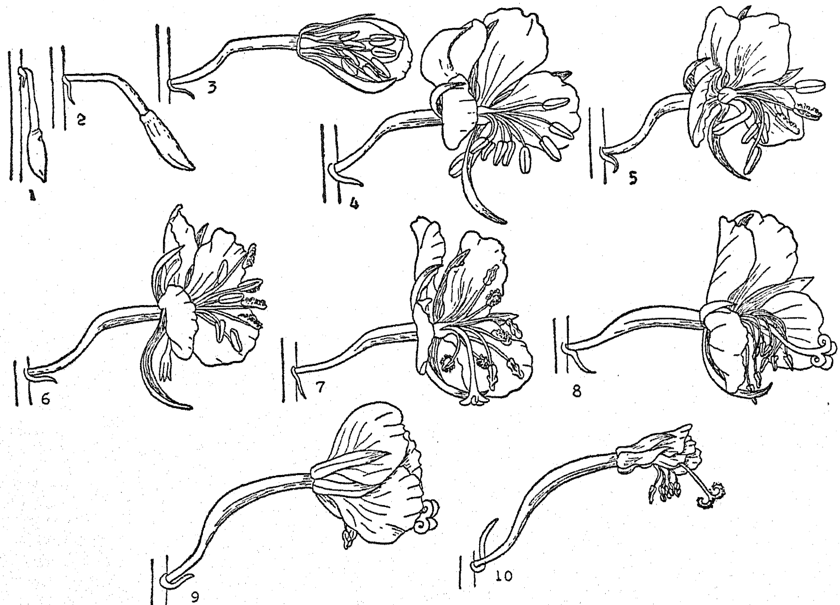

FIG. 29. THE POLLINATION STORY OF THE FIREWEED

also by the red sepals and the green pollen of the anthers. One of the lower petals or the style is the usual landing-platform, but in many flowers a petal has been swung into a central position below to serve for this special purpose. A large amount of pollen is produced by each flower, chiefly because of the numerous ovules to be fertilized, but partly also because it lacks protection against robber insects and against rain.

Bumble-bees do most of the work of pollination in the fireweed, though it is frequently visited also by the honey-bee and

many other bees and butterflies. The bumble-bee is chiefly interested in securing nectar, but usually gathers some pollen, and occasionally devotes its attention to this alone. It has formed the habit of alighting in the lower part of the flower cluster and working upward, since the blossoms open from bottom to top. In the stamen stage the bee lands on a lower petal or even on the group of stamens and quickly moves into a position where its tongue can reach the nectar. As it sucks the latter, its hind legs are busy packing pollen away in the baskets on them, while its brisk movements shower pollen-grains all over the hairs of its body. When it comes to a flower with the stigmas recoiled and receptive, it often straddles the style, thus touching the stigmas, or brushes past a curled tip as it passes from petal to nectary. In the rare cases where the stigmas are not dusted with foreign pollen, self-pollination is usually brought about by the closing petals, which bring the dry anthers with their few remaining pollen-grains near to or in contact with the stigma tips.

More than once a doubt has been expressed as to whether the corolla really does serve to attract insects, and experiments have been carried out to test this in the fireweed. When the petals were completely removed from certain flowers, less than half as many visitors came to them. In the case of the wild geranium, which in many other respects resembles the fireweed in its behavior, pulling off the petals caused the visits to cease entirely and cutting them back to a fourth of their width decreased visits more than half.

GREEN GENTIAN

The green gentian resembles both the fireweed and geranium in bearing regular open flowers, but the details of its structure and behavior are quite different. When the blossom first opens, the petals are upright and the stamens are crowded around the style, with the faces of the anthers turned inward. A few hours later the petals have spread out, the stamens have separated somewhat and the anthers are turned upward. The petals continue to flatten and the stamens slant outward at the top, while

the anthers have turned their faces away from the stigma. One of the anthers now quickly cracks open and is followed in a few hours by the one directly opposite. As the pollen is removed from these, the third opens and then the fourth, the filaments of the first two meanwhile carrying them down and out of the way. As the second pair moves downward, the stigma becomes receptive and the flower remains in this stage for a day or two.

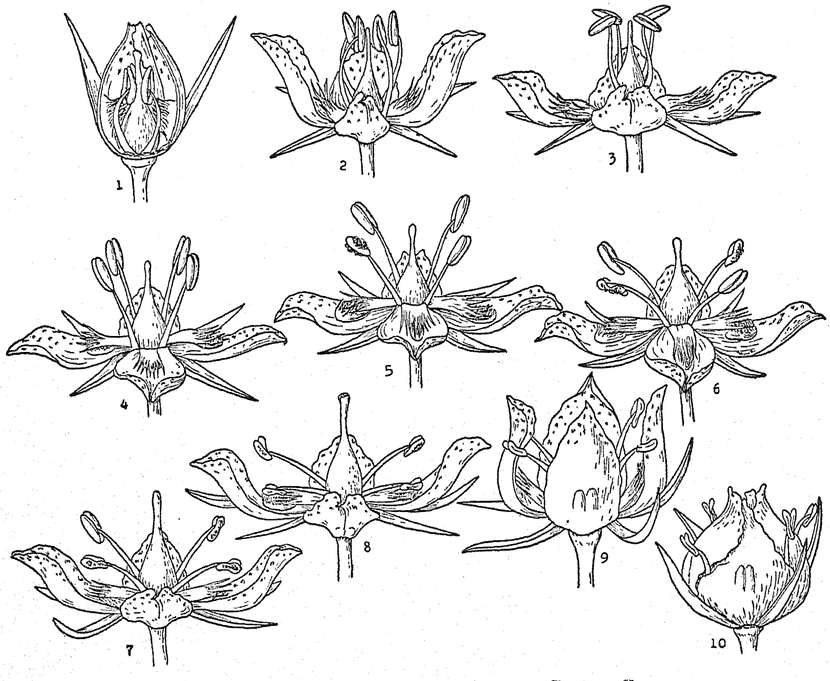

FIG. 30. THE POLLINATION STORY OF THE GREEN GENTIAN

The petals and stamens then begin to move upward, followed more leisurely by the sepals. The petals finally close together so tightly that such flowers are often mistaken for buds until the withered stamens are seen projecting from the edges. The fresh green color fades and the wilting petals begin to crumple.

In spite of the uniform gray-green of this plant, it is readily found by bumble-bees and honey-bees. This is probably because of its tall sentinel-like form and the huge flower-clusters, which

sometimes reach a length of four feet. The nectar is abundant and apparently it is also unusually pure and delicious. It collects in a pit-like nectary tightly covered by a fringed scale, and is almost perfectly protected from rain and dew and from small poachers.

The bumble-bee and honey-bee visit the green gentian almost wholly for nectar, but occasionally one of the latter scrapes the pollen out of the anthers in turn and packs it on the hind legs. Every petal makes a convenient landing-platform, as the nectary is directly in front of the bee as it alights, and it needs only to push the lid aside to sip the nectar. The reward is too great to permit slighting a single nectary and the bee is practically certain to rub against one or more of the anthers at each visit. It is less certain to touch the small stigma in the later stage, though the bee sometimes lands on the pistil and touches the stigma with the abdomen. The stigma is still receptive as the petals and stamens close and consequently the chances are greater of its being touched by a visitor. The lure of the nectar is so strong that the bumble-bee often lands on closed flowers and forces its head beneath the edge of a petal in order to reach the nectar. The behavior of the anthers makes it practically certain that self-pollination will not occur until the petals begin to close, bringing the anthers and stigma more or less into contact.

The bumble-bees were at first much confused when the petals were trimmed closely about the nectary and replaced by false ones made by gluing bluebell petals to the sepals. The absence of the usual landing-platform bothered them on arriving and when they finally landed on the false petals, they tried to find the nectar between these and the sepals. In every case the nectary was eventually located, but only after much searching. The honey-bees flew near enough to inspect these changed blossoms, but hurried off without alighting on them.

MONKSHOOD

The monkshood goes about its work in much the same way as the larkspur, of which it is a near relative. As the bud

enlarges, the anthers peep out from the lower edge of the sepals and the group of thirty or more is disclosed as the sepals curl back. The two upper anthers are usually the first to open, apparently because they are in the direct path of bees seeking the nectaries. Two of the lower anthers may split next and the work of maintaining a constant supply of pollen for removal continues for four or five days. After the innermost stamens

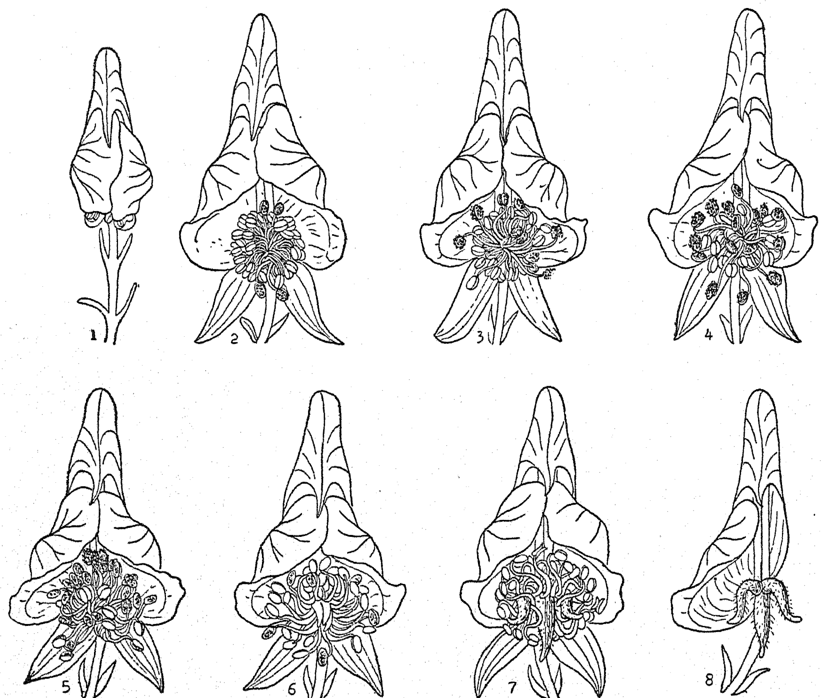

FIG. 31. THE POLLINATION STORY OF THE MONKSHOOD

have shed and the dried anthers have moved to the outer edge of the flower, the three stigmas appear in the middle in line with the nectary openings. They are quickly pollinated and the tips of the young pods soon emerge from the mass of stamens, which begin to dry up and drop off. This is followed by the falling of the colored sepals and the three horn-like pods are all that remain of the flower.

Attraction by color in the monkshood devolves entirely upon the sepals, which are usually deep blue-purple, though they are sometimes white. The two petals have been converted into sack-like nectaries with long tubes leading from them, which render the nectar inaccessible to practically all visitors but bumble-bees. They are almost completely hidden by the characteristic hood, and the nectar is thus doubly protected against rain as well as marauders. The large amount of pollen is also an attractive feature of the flower and this too is well protected by the arching over of the lateral sepals. A definite landing-platform is lacking, but the lower sepals meet this need in a large measure.

The visiting bee lands on the lower sepals or the stamen mass with its head toward the base of the nectaries. It empties these in succession, its body meanwhile becoming dusted with pollen which is usually transferred to its legs before it leaves the flower. When it enters a flower in the pistil stage, some of the pollen on thorax or abdomen is left on the receptive stigma and fertilization ensues. There is no special device for self-pollination, but this may result from the proximity of anthers and stigmas as the bees trample over them. The value of the colored calyx in attraction has been confirmed by experiments in which the hood was split and folded back, such flowers receiving relatively four times as many visits as the normal ones. When paper imitations were placed among the flowers, they were never visited with the exception of the pale-blue and white ones, but flowers painted with water-colors were frequently sought.

NODDING ONION

The blossoms of the wild onion are borne in a nodding cluster on the end of a slender, flexible stem. Their delicate beauty suggests their relationship to the lilies, even if the odor of the leaves does not. At the time of blooming the pink buds hang straight down. The tips of petals and sepals part slightly and reveal a single anther, which soon pushes out on its slender filament. In an hour or two this bursts open and at the same time a second anther joins it; meanwhile the flower itself begins to rise on its stalk. The first stamen then dries and shrivels,

the second scatters its pollen and the third pushes out ready for its turn. The flower continues to swing upward and has reached the horizontal position about the time the fifth stamen has appeared. By the time most of the pollen has been removed from this, the sixth stamen is ready to take its place, and the style may be seen in the midst of the twisted filaments. In the next stage the oblique flower has lost most of its anthers, the filaments are shrunken and the style has carried the receptive

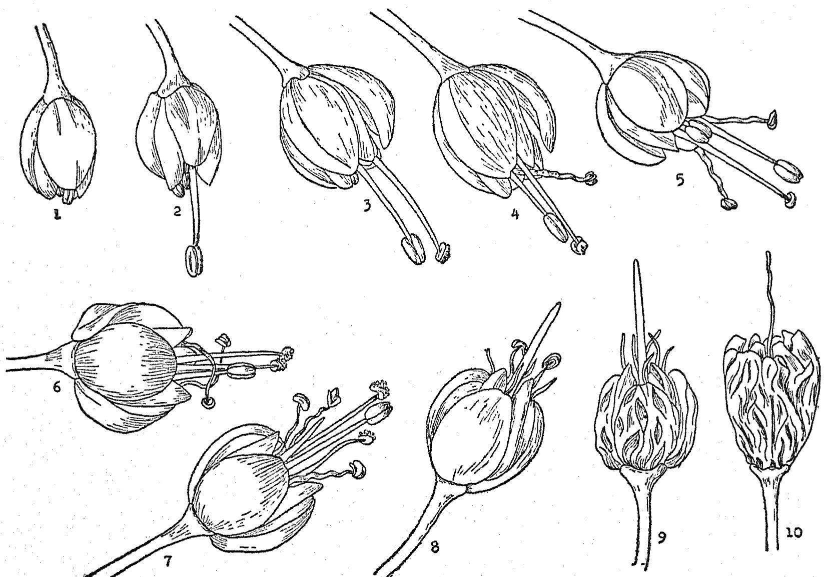

FIG. 32. THE POLLINATION STORY OF THE NODDING ONION

stigma into the position occupied in turn by the shedding anthers. After a day or two the flower becomes erect and the anthers have all fallen. The petals begin to wrinkle, and soon afterward the style withers and the petals dry closely about the enlarging fruit.

The onion owes its attractive power to the bright pink of the corolla-like perianth and to the relatively abundant nectar flow, as well as to the faint perfume. The hanging flowers afford fairly adequate protection to the nectar, but little or none to the

projecting anthers. No landing-platform has been developed, though the shape and position of the flower render landing a matter of slight difficulty. Bumble-bees are especially fond of the nectar of this flower and may be found working on the clusters long after sundown. They alight on them from below and the under parts become well dusted with pollen as they probe for the nectar. Since the stigma later takes the place occupied successively by the anthers, the bee is practically certain to deposit part of the pollen load on this when it goes to such flowers. Under the usual conditions, self-pollination is difficult if not impossible, but the great abundance of fruits testifies to its unimportance.

WHITE EVENING-PRIMROSE

The evening-primrose affords a striking contrast to all of the previous flowers by virtue of the large size of its blossoms, the

FIG. 33. THE POLLINATION STORY OF THE WHITE EVENING-PRIMROSE

white color and the habit of blooming at night. It grows in families on warm gravel banks, the large buds springing directly from the rosettes of leaves. Few flowers equal it in the rapidity with which it opens, often no more than two minutes elapsing between the first loosening of the petals and their complete expansion. With the passing of the heat of afternoon, the slowly swelling corolla forces the calyx tips apart and the four tips of the stigma lobes peep out of the tube. In the course of an

hour they are pushed free and take a horizontal position. By this time the petals are in active motion and they quickly unroll and flatten out, freeing the stamens from which the pollen hangs in long golden strings. The anthers all shed at once, since the flower lives but a single night and pollination must take place within a period of a few hours. The blossoms remain open all night, but a few hours after sunrise the petals turn pink and gradually close, finally wilting into a flat mass that dries during the day.

Like so many night-bloomers, the evening-primrose is visited chiefly by humming-bird or sphinx moths, though other nocturnal moths are occasional visitors. These are guided in the dusk or at night by the white corolla, though the great attraction is the deep tube half full of fragrant nectar. This tube is open to the rain and to wandering insects of all kinds, but the habit of blooming at night is an almost complete protection against both. The broad flat petals might serve as admirable landing-platforms, but these are wholly unnecessary since the habitual visitors poise above the flowers without alighting.

The two larger moths that visit this flower have a tongue or proboscis often four inches long, which enables them to empty the deepest tube, but the common humming-bird moth with a tongue but two inches long can secure only a small part of the nectar store. The moth flies like an arrow to a cluster of flowers, hovers over one and unrolls its proboscis. It gradually descends until the tip of the tongue is just above the tube; after an occasional false start the tongue is inserted in the nectar and the moth slowly sinks as the nectar is lowered. The nectar exhausted, it poises above the next flower, its long tongue spangled with golden dots of pollen. As this probes the tube, it often touches the sticky lobes of the stigma and leaves the pollen-grains on them. On colder nights in the mountains the sphinx-moths rarely fly and such flowers as open then must have recourse to self-pollination. However, this is practically certain, since the closing of the corolla brings the stigma-lobes in contact with the pollen hanging in long threads from the anthers.

BLUE PENTSTEMON

The blue pentstemon of the mountains is often called beard-tongue from the fifth stamen, which has lost its anther. In place of the latter it has developed a tuft of hairs, plainly visible in the mouth of the corolla. At the time of blooming the lobes of the corolla loosen until the two lips are free. The upper lip, consisting of two petals, assumes a more or less erect position, while the lower one of three petals spreads out into a broad platform. At this time the two pairs of anthers lie against the roof of the corolla tube, while the fifth stamen or staminode is in line with the middle petal of the lower lip. The upper or outer pair of anthers splits first, usually both at the same time, and the pollen is scraped out within a few hours. The second

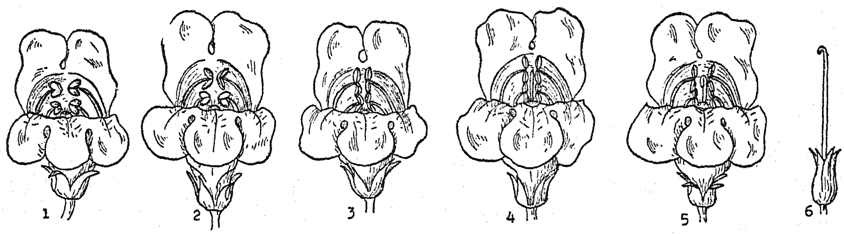

FIG. 34. THE POLLINATION STORY OF THE BLUE PENTSTEMON

pair bursts the next day and the upper ones spread their halves and begin to shrivel. By the next morning the halves are in a straight line and the same process begins in the lower pair. Meanwhile the style has been pushing the stigma forward and this has reached the upper pair by the time the pollen is all shed. The style then curves sharply downward at the tip and carries the receptive stigma into the position where pollen can be most readily deposited upon it. After a day or two the corolla shows signs of fading and it slips off, leaving the style behind still fresh. At the same time the lobes of the calyx close tightly about the ovary, and the style begins to shrivel as the latter grows into the pod.

In spite of the three-fold attraction of its deep blue color, nectar and pollen, the beard-tongue is visited less than one would expect and chiefly by the so-called mason-bees. Landing

is admirably taken care of by the broad lower lip and guidance is secured by the groove of the middle lobe and the bristly hairs on either side of it. Much more important, however, is the staminode which lies directly in the visitor's path and forces it up so that it touches the anthers or stigma as the case may be. The form of the corolla and its horizontal position serve for the protection of both pollen and nectar.

From the large number of bees that ignore the nectar, it would seem that the pollen of the beard-tongue must be esteemed as a special delicacy. The favorite method is to rub the back of the thorax against the anthers, often so vigorously that a scratching sound is distinctly heard. Bumble-bees land in the usual way and then turn upside down, the front legs scraping the pollen out of the anther halves and packing it on the hind ones. When the bees enter flowers with the stigma receptive, they are practically sure to dust the latter with pollen. Those visitors that enter the flower for nectar are forced upward by the hairy staminode so that they are sprinkled with pollen in one flower and leave some of this on the stigma of another. Self-pollination seems to be seldom required, but can be brought about as the corolla falls off, by the narrow base of the tube bringing the stigma in touch with the staminode on which some pollen-grains have fallen.

When the flowers are turned upside down, bees land readily enough on the upper lip, but some of them fail to realize the significance of the change and rub against the staminode in the endeavor to collect pollen. In flowers with the lower lip removed or the lobes separated, the difficulties of landing were met by the various bees very much as human individuals solve problems. Some were able to enter the flowers with only a moment's hesitation, others made several ineffectual attempts before they succeeded, and still others flew away without nectar or pollen, evidently discouraged.

MONARDA

As the most highly specialized and most efficient of the insect flowers we have been considering, the horse-mint appears to

achieve its results with the minimum of effort. As the blossoms open, the two lips separate and the single pair of anthers crack almost immediately. By the next morning the pollen is nearly all shed and the style has appeared. A few hours later the shrunken anthers have fallen forward and the two stigma tips occupy the same place, ready to receive pollen. By evening or early the next day the lips of the corolla begin to twist and wither, and the stamens leave the shelter of the upper lip. The whole flower then wrinkles as it wilts, the stigma tips closing and dropping about the anthers.

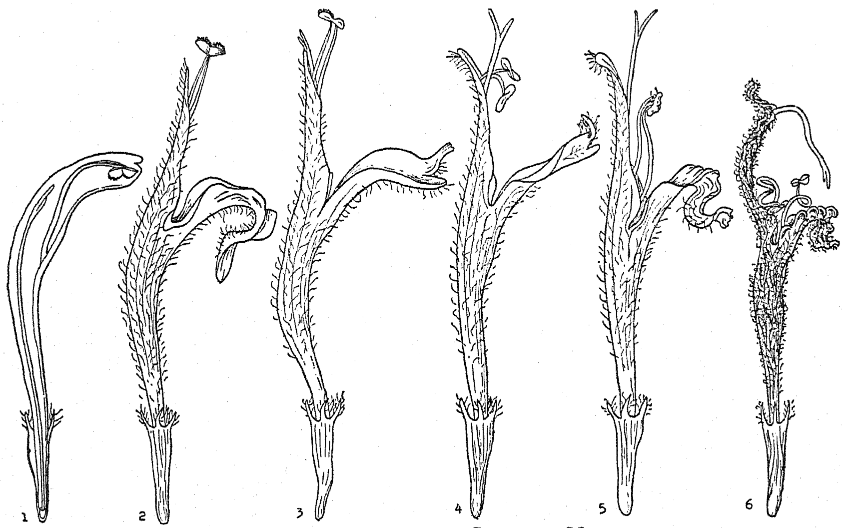

FIG. 35. THE POLLINATION STORY OF MONARDA

The color attraction of the corolla has been greatly enhanced by the grouping of the flowers in a dense cluster, resembling in several respects the head of a sunflower. The nectar is eagerly sought by a host of visitors and some bees devote themselves to gathering pollen alone, though these are mostly short-tongued ones that can not reach the nectar. The lower lip forms one of the best of landing-platforms and the groove in it guides the visitor to the nectar in the shortest possible time. The upper lip also has some share in guidance, but it serves chiefly to

protect the anthers and the styles while they are young. The long narrow tube makes the nectar inaccessible to all but the larger bees and the butterflies, and with the aid of the upper lip also protects it against rain and dew.

The larger bees and the smaller butterflies land on the lower lip and force the head into the opening of the tube in the endeavor to get all of the nectar. In doing this they first touch the anthers of flowers in the earlier stages and then the stigmas of the later ones. The larger butterflies, such as the silver-spots, land in the center of the head as a rule and the long tongue is guided down the tube by the base of the upper lip. One species of small bees lands on the anthers and devotes its whole attention to collecting pollen, while another poises in front of them and stows the pollen away at an amazing rate. Humming-birds are frequent visitors, darting from cluster to cluster with lightning-like rapidity and perhaps serving as the most effective pollinator of this species. They are especially attracted by the bright red flowers of the paint brush, but after this is past blooming, they go to nearly all flowers with long narrow tubes in which the nectar lies too deep for most insects.

Bumble-bees often bite holes in the base of the corolla and steal the nectar without rendering an equivalent in pollination work. They do this even when they can reach the nectar, probably because they can get it all in this manner. One summer the individuals of a certain species punctured all the flowers visited in one group, but landed and sipped nectar in the usual fashion at those of another near by. The relative importance of the lips in promoting pollination is suggested by the fact that only 11 visits were made to flowers with both lips removed, to 58 visits to those with the lower lip cut off and 220 to blossoms with the upper lip alone removed.

Wind Pollination

RIBBON PLANTAIN

The plantains are apparently recent recruits to the group of wind-pollinated plants. They still possess a corolla, but it is dry and papery and seems to be in the process of disappearing.

In the common plantain of the door-yard the stamens are short, but the ribbon plantain hangs the anthers out on filaments of unusual length. The spikes are also borne on long stalks that facilitate the removal of the pollen by the wind. The first sign of blossoming is the projection of the style tip beyond the bract that covers each flower of the lowest row. The styles grow

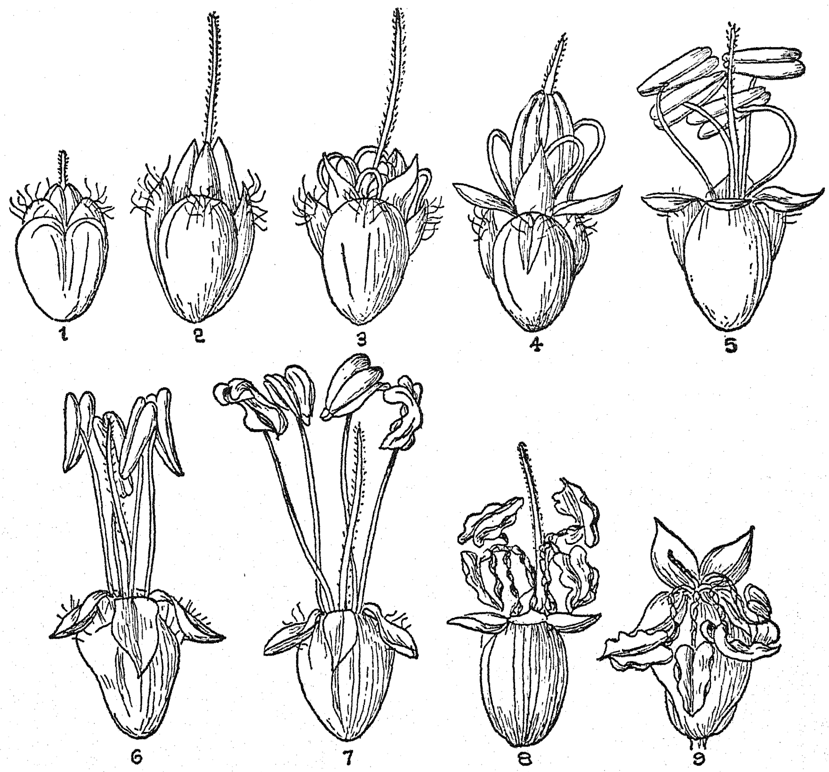

FIG. 36. THE POLLINATION STORY OF THE RIBBON PLANTAIN

steadily on warm days and in a day or two reach full length, meanwhile the flowers of the second row have extruded their stigmas. On the morning of the third day as a rule, though much depends upon the amount of sunshine, the anthers begin to push out in a column, which soon separates at the tip, showing the loops of the filaments. These appear to serve as springs

to force the anthers out fully, while the petals become erect and then spread out flat. The exserted anthers are first horizontal and then are carried into the upright position by the straightening filaments. The complete series of stamen movements usually requires one to two hours on a warm summer morning, though the motion is sometimes sufficiently rapid to be noted by the eye. Once extended on the long filaments, the anther cells crack open and small showers of pollen are shaken out by gusts of wind. The stigmas have usually withered before this, though sometimes they remain fresh and apparently receptive until the anthers open. The flowers of the two or more rows above have stigmas ready to receive the pollen, though most of it is blown to other spikes or plants. By the middle of the afternoon or by the next morning at the latest, the anthers are empty and the filaments begin to shrivel. This process continues rapidly and soon the stamens form a tangled mass over the petals. They fall in a day or two, exposing the brown recurved style and the petals. The style then soon falls away, but the dry petals remain expanded until the entire corolla is pushed off by the growing pod. Cold rainy weather may retard the steps of the process so greatly that the usual cycle of two or three days may require a week or more.

GOOSEFOOT OR LAMBS-QUARTERS

Like many other wind-pollinated flowers, the goosefoot exposes its stigmas first, while the calyx is still closed. The first day they are short and erect, and on the second they elongate and diverge, thus increasing the chances of catching pollen-grains. On the morning of the third day if it is sunny, the frosted sepals part and a circular opening appears, showing the inner edge of the anthers. In an hour or two these become visible in a close ring and by noon the filaments have elongated to carry the anthers above the sepals. About this time one or more of the anthers crack and expose the pollen for removal by the wind. The sepals gradually spread more widely and the filaments move with them, thus permitting readier removal of the pollen. Usually the stigmas have become shrunken and

brown by this time and self-pollination is prevented, but occasionally the stigmas lag and appear with the anthers. As the temperature drops in the afternoon or with increasing cloudiness, the sepals close again and crowd the stamens together in the center. If the stigmas are still receptive at this time, self-pollination is almost unavoidable, though it is regularly rendered unimportant by cross-pollination during the day. The following morning, unless cold or rain prevents, the sepals open widely, the filaments flare as a result and the remainder of the pollen is blown away during the day. Towards evening the filaments

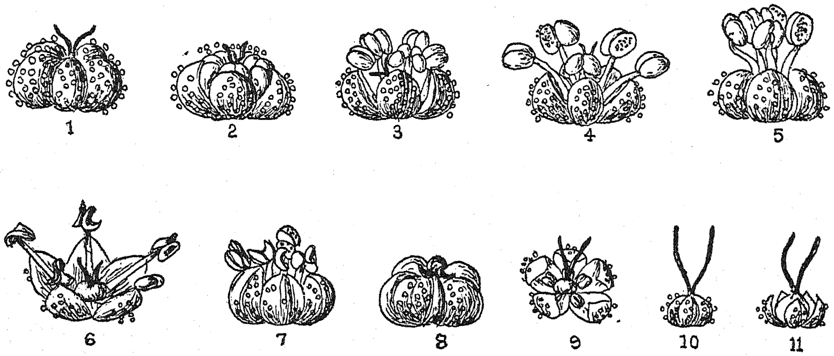

FIG. 37. THE POLLINATION STORY OF THE GOOSEFOOT

shrink, the calyx closes finally and the shrunken anthers persist for several days at the center. The calyx then remains closed until the fruit ripens, serving both to nourish and protect the latter, while in some relatives, such as the salt-bushes, it is greatly enlarged to form scales or wings for distributing the seed-like fruit.

The goosefoots resemble other wind-pollinated genera, such as maples and ashes, in being in the midst of an active evolution of the flower. In the same cluster may be found perfect flowers and those with pistils alone, while here and there a flower with good pistil but imperfect stamens indicates the course of development.

TIMOTHY

Unlike most of our common grasses, the timothy has no special device for opening the dry hard scales that enclose the flower. The evening before it is ready to bloom a tiny crack may be seen at the tip of many of the flowers and the purple anthers show through the scales. Shortly after sunrise, this crack has widened to an irregular hole and the column of three anthers begins to push through it. When the anthers are nearly out, they separate slightly, disclosing the two feathery stigmas tightly closed together. In a short time the anthers are carried out on the ends of the long filaments and the stigmas spread at the base. At this stage the green spike is a beautiful sight with its

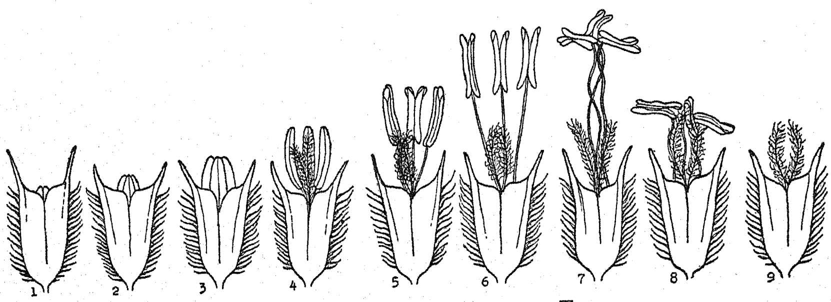

FIG. 38. THE POLLINATION STORY OF TIMOTHY

garment of purple. The anthers soon crack open and the slightest touch or breath of wind sends a cloud of pollen into the air. Towards the middle of the morning on a warm day, some of the filaments begin to shrivel and twist and a few anthers fall, while by noon the filaments and anthers have collapsed in a mass against the green spike. The anthers fall off rapidly and the filaments dry and disappear, leaving the spike feathery with the short white stigmas. The latter begin to dry and collapse by mid-afternoon and have shrunken against the spike by the next morning.

In warm sunny weather the remaining flowers open betimes the next morning and the spike is again a mass of stamens and stigmas. In some, one-half of the spike is feathery, while the

other still retains its mantle of shrunken filaments and stigmas. On the third morning a few belated flowers may open, but they are merely stragglers to show that the period of flowering is over.

The rye-grass differs from the timothy in being an evening bloomer, the lower flower of each spikelet of the spike opening with its companions about 5 o'clock, the yellow stamens hanging out in distinct groups of three. The stigmas appear more slowly, but remain the next morning after the anthers have fallen. This is repeated each warm evening, until the several flowers of each spikelet have opened successively, when the spike again closes together. The grasses with much branched clusters or panicles usually open one at a time, some of them even delaying until mid-day or later. Some grasses of this kind have flowers that open and close for two or three days, the stigmas usually appearing the second morning.

COTTONWOOD

The pollination behavior of most of our common shade and forest trees is simple, though it differs much from one species to another. These differences are chiefly in the form of the flower clusters and in their arrangement on the plant. The clusters may appear as knobs on the naked branches as in the ash, in open hanging racemes as in the box-elder, or in long swaying catkins as in the cottonwood, willow and others. In the walnut, oaks, beech and chestnut, the stamen flowers are in catkins, but the pistillate ones are in small inconspicuous groups or even single. The pines and their relatives bear the stamens in dense clusters at the ends of the lower branches, while the seed-bearing cones are usually higher in the tree and often at the very top. The larger number of our common trees have the staminate and pistillate flowers on the same tree, but some, like the ash, box-elder, cottonwood and willow, have them on separate individuals.

In our common cottonwood the staminate and pistillate catkins appear almost together, but the staminate are so much larger and so much more conspicuous in their red-brown garb that the pale greenish-yellow of the pistillate ones is hardly

noticed. As the axis of the staminate catkin stretches, the many stamens of the lowermost flower crack open and free the pollen for its flight. This process moves along the axis for two to several days, the stamens shrinking and drying as they become empty. Finally, the stalk itself shrinks and loosens, and the next rain or wind carries thousands of crumpled catkins to street and sidewalk. Meanwhile the scalloped stigmas have capped the ovary like a tiny garland, catching the flying pollen-grains in their folds. Fertilization causes the ovary to grow rapidly into a green pod and the catkin becomes more visible as it lengthens

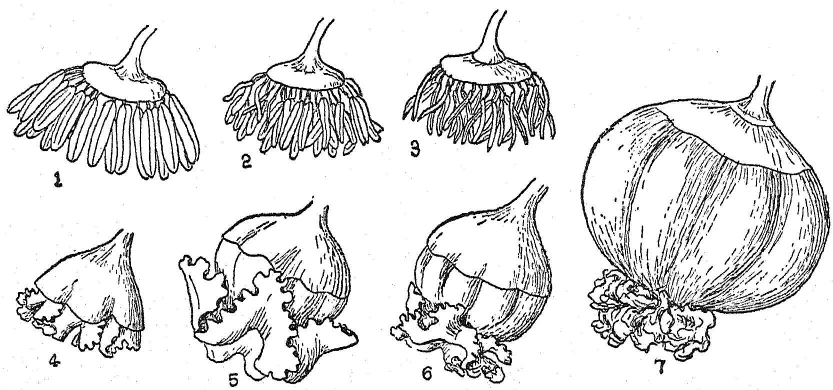

FIG. 39. THE POLLINATION STORY OF THE COTTONWOOD

among the young leaves. In a few weeks the pod splits into three valves and the seeds take off in a flying squadron of silken parachutes.

EMERGENCY WORK AND OVERTIME

GROWTH AND SURVIVAL

Just as in all human affairs, the day's work of flowers goes smoothly under the usual conditions, but a sudden change in these may completely upset the habitual routine. Plants have their ups and downs like people and like them too there is always a cause to be found for these, if one takes the trouble to look carefully. Most of these disturbances are trifling and produce only a fleeting effect on the ordinary routine, to the extent that the work is done more slowly or less efficiently, or sometimes

in undue haste. Occasionally, the change in the plant's surroundings is so abrupt or intense or so enduring that its usual habits of work are broken for a long period or even completely destroyed. As we shall see later in detail, the plant may adjust itself for the time to the new conditions, returning to its old habits when the crisis is past; it may suffer great changes in its behavior or structure, or under exceptionally hard conditions it may perish. The story of plant evolution and relationships is an account of the manner in which plants have met such emergencies and the degree of success they have achieved in doing this.

Most emergencies affect the plant body directly and are felt by the flower only inasmuch as it is a part of the plant, many of them being met and solved successfully or otherwise before the plant comes into bloom. Those that occur while the plant is in blossom frequently leave their impress on the flowers, but these seem to be most strikingly changed by the crises that touch them directly, as one would expect. The two kinds of emergencies are quite different, as the plant is affected most by those that strike at its water supply and its power to make food and to grow, while the flower is more concerned with the agents that bring about pollination, the conditions that control the setting and ripening of fruit and the manner in which the seeds are scattered.

Every one who has cared for a garden understands the nature of the emergencies that growing plants must meet. While it is quite possible to recognize some emergencies as favorable and others as unfavorable, as a matter of fact the latter are the only ones that ordinarily need to be taken into account. Water, heat and light are the most important factors to the growing plant, but in field and garden light usually becomes a decisive matter only when plants are overtopped by others. The most frequent emergencies in plant life arise from unfavorable amounts of water or temperature. Too much or too little of either is bad, but not equally so; at least, too much water or too much heat occurs much more rarely than the reverse. For most plants the real crises are drouth, frost and "hot waves," though insects and

FIG. 40. ADAPTATION FORMS OF THE ROSE GENTIAN

(1) Alpine Dwarf; (2a) Normal Shade; (2b) Dry Shade; (3a) Drouth; (3b) Normal Sun

fungi also play major rôles. During a drouth plants fail to grow properly, or they wilt and die for lack of water. A hot wave operates in a similar manner, but much more quickly. Within two or three days it may "burn up" a corn field completely, not by intense heat but as a consequence of the hot dry wind, which causes the plants to lose water more rapidly than it can be drawn from the soil. The damage caused by "Jack Frost" is due to actual freezing of the tender watery parts of plants. Native plants have become so habituated to frost in early spring and in autumn that it seldom constitutes an emergency for them, but in northern regions gardens are each year blackened by frost before their blooming is past.

Such emergencies are matters of climate and in consequence each region is characterized by its own peculiar kind. The Southwest is often spoken of as desert, because all the native plants in it bear the impress of drouth, which recurs each year in some degree and is a crisis of the first magnitude at intervals of a few years. In the East, on the contrary, a serious drouth is all but unknown; the rainfall is relatively high, but the excess is seldom great enough to cause an emergency. Even in this case it is the shortage of air in the soil rather than the abundance of water that make drainage necessary for cultivated fields. The plants of the South and the Pacific Coast experience killing frost but once in a decade or so, those of the North and of mountain regions may be subjected to repeated frosts every year. Indeed, on such high summits as Pikes Peak, buds and flowers may be coated with hoar-frost night after night and still go about their usual work the next day.

FLOWERS AND BLOSSOMING

Conditions that retard or promote the growth of the plant body are usually reflected to some degree in the flowers, though the effect may sometimes be exactly reversed. When the environment is exceptionally favorable to growth, the plants may "run to leaves" and it becomes necessary to cut them back or prune them severely to force them into blossom. A similar result may be obtained by cutting off the water supply and thus check-

ing growth, and for much the same reason potted bulbs are kept in a cool cellar for a month or two before forcing them. There is thus a certain measure of antagonism between the leafy shoot and the flower cluster, so that if either obtains an undue advantage the other is correspondingly hampered. However, within fairly wide limits, plants that make the best growth produce the largest or the most abundant flowers, and factors that stunt the plant body also diminish the size or number of the blossoms. The most striking exceptions are perhaps to be found in shady places, the weaker light causing the plants to grow tall and slender, without enabling them to make sufficient food for abundant flowering. When plants are crowded together, the keen competition for water makes them tall and spindling and has a marked effect in reducing the flower cluster. The damage caused by weeds is also a consequence of competition. The sunflowers of a corn-field use water almost three times as rapidly as corn and correspondingly diminish the amount available for the growth of the latter. The parasites that afflict plants, whether insects or other plants such as mistletoe, dodder or rusts, diminish their vigor and usually have a like unfavorable effect upon blooming.

The countless multitude of plants that spring up anew each year go through the regular work of the growing season in spite of most emergencies. They may have to work harder, keep at work for a longer time or stop for winter with a smaller output or a scantier store of food, but the even tenor of their lives is not profoundly disturbed. But when the crisis touches the flower directly, the effects are much more immediate and the changes more serious. A late frost in spring may cause buds to open tardily if at all, or it may destroy the delicate anthers or stigmas and thus render fertilization and the production of fruit impossible. Continued cold weather in early autumn may keep buds closed, producing the closed flowers in which self-pollination is alone possible. This habit once formed, it sometimes persists and becomes a constant feature of certain violets, and of the touch-me-not and Venus' looking-glass. It is sometimes brought about also by excessive rains and especially when the

water level of pond or stream rises too high for a considerable period. When the seeds of sun plants are carried into deep shade, the flowers usually undergo striking reduction in number and size and often in color also. If the flow of food to the cluster or the individual flowers is reduced by accident or design, the size may be greatly decreased and the color may completely disappear. Flowering stems are frequently bent or partly broken and plants are trampled in such a way that the position of the flowers is changed, especially in relation to the effect of gravity. As a result, they twist about in the endeavor to resume the former position and in so doing are often changed in striking manner. Similar changes have been brought about experimentally and these seem to throw light upon the way in which flowers have become two-lipped or otherwise irregular, as in the snapdragon, mint, orchid and sweet-pea.

POLLINATION EMERGENCIES

As we shall see later in detail, the most striking differences in the looks as well as the structure of flowers are connected with the method of pollination. The correspondence between the form of the flower and pollination by insects on the one hand or by wind on the other is so close as to leave little doubt that they are effect and cause. Experimental proof of this relation is difficult to obtain, though recent studies indicate that it will be forthcoming in time. Since the first and simplest flowers have attractive petals or sepals and often nectaries as well, we need only look for emergencies through which these have become wind-pollinated. The grasses and sedges, as well as most of our common trees, such as elms, oaks and willows, suggest that this was the consequence of their living in open wind-swept meadows and prairies or of being tall enough to catch the breeze. Even the insect-pollinated garden plants and orchard trees have their pollen blown about more or less by the wind and this helps to explain how position or height might gradually result in changing a flower from insect to wind pollination and thus profoundly modify its appearance and structure. Windy stretches are also the most difficult ones for the flight

of bees and butterflies and hence seed-production and survival might often come to depend upon the successful transport of pollen by the wind. Rainy days and seasons also handicap pollinating insects and may have played some part in the change to wind-pollination, though a frequent recourse under such conditions has doubtless been self-pollination.

In a sense, emergencies may arise in the flower cluster or the flower itself, though these might rather be regarded as opportunities. These are most readily seen and understood in the case of cultivated plants, which are so treated by the florist as to enhance size, color, or some particular form. The marvelous development of the chrysanthemum and dahlia within a generation or so are outstanding examples of this, but nearly all the garden favorites exhibit it in some meaure. In the competition between buds for food, position or size often determines that some will grow and others will not. The florist takes advantage of this fact to remove all the branches from the main shoot or all of the buds from this but one and thus obtain the largest and most perfect flower possible. The significance of this is best seen in the comparison of one of the earlier varieties of chrysanthemum bearing several hundred small single heads with the more recent Japanese sorts displaying a solitary double head almost a foot across. This process is much less evident in nature, but it is constantly in operation, producing changes of greater or less importance.

When confronted by an emergency, flowers are like other living things in that they may solve the difficulty or may fail to do so. If the situation is a critical one, the flowers will change and continue to produce seeds, or they will "sit tight" and either make no seed or only poor or scattered ones. In the one case, the species will become increasingly successful under the new conditions, while in the other it will gradually or quickly disappear. Since critical emergencies almost never occur over the whole area occupied by a species, it seems clear that the latter may drop out in one region, become modified in another and persist unchanged in a third. This takes into account all the possibilities and may be regarded as the usual rule in evolution.

It is probable that it has been exemplified in the case of the buttercups in particular. Some of these were long ago changed into roses, poppies and arrowheads, others disappeared in the struggle for existence during past ages and still others have remained buttercups through the changing cycles of years. This is equally true of the great centers of evolution that have sprung from the buttercups, namely, geraniums, roses and lilies. Though they arose in the remote past, they are still among the great orders of flowering plants today, while in the meantime they have also given rise to all the other groups of flowers. The special ways in which the many flower families have met their particular emergencies have been worked out in the course of their life experiences and this forms the theme of the next chapter.

EFFICIENCY IN FLOWERS

When one calls to mind the great number of different flowers and considers the striking contrast between roses and grasses or orchids and walnuts, it is at first hard to realize that they are all flowers and devoted to the same work. It is this difficulty that has given rise to the popular opinion that most trees and grasses do not bear flowers. This is seen to be a mistake when it is remembered that fruit and seed are only the final product of the flower, but it is easily explained by the small size and green color of the flowers of the grasses and grains and of our common shade trees. Even after one knows that all of these are flowers, it seems that they must be built of very different parts, and it is a complete surprise to find that this is not the case. The blossom of a grass contains stamens and pistils just as does that of a rose, while the unlikeness of a buttercup and a snapdragon is due merely to the difference in the experience of the same four parts, namely, calyx, corolla, stamens and pistils. In short, the great majority of flowers consist only of these four working parts, though many others have lost one or more of these, as the maples are doing at the present time. At first thought it seems incredible that thousands upon thousands of different kinds of flowers should differ only in the behavior or number of these fundamental parts, but a comparison of dis-

similar blossoms enables one to understand this. A columbine, sweet-pea and phlox look exceedingly unlike, but a careful examination shows that they all have sepals, petals, stamens and pistils, more or less changed to suit their different ways of working.

Although the chief work of the flower is to produce fruit and seeds, most of its tasks center about pollination. In consequence one would expect the forms of flowers to be the result of different ways of securing pollination, and this is the case. The flowers that resemble each other least are such as irises, hollyhocks and butter-and-eggs on the one hand and oaks, ragweeds and grasses on the other. The former have brilliantly colored corollas and are attractive to insect visitors; the latter lack the corolla and are tiny and green, so that they must resort to the wind. Hence, the greatest differences between flowers arise out of the pollination agent they employ, and this is the reason for distinguishing all flowers as insect-pollinated and wind-pollinated. This is the most important of distinctions and has a profound significance in evolution and relationship.

CONSERVATION OF ENERGY AND MATERIAL

Plants are like all other living things in having to do their work with a limited amount of material and energy, and even of time. These limits may be narrow or wide, but the plant is compelled to practice economy within them, if it is to be successful. This does not seem to be true of such trees as the willow and oak, which apparently scatter their pollen in the wind with reckless prodigality, but we shall see that they have already saved for this very purpose. The law of conservation applies to both plant and flower with such force that the doing of anything new nearly always means changing or losing some old habit. If three petals are enlarged to make a landing platform, some other part or parts must get along with less material and will diminish in accordance. Nearly all of the more efficient or specialized flowers show clear evidence of this balance between parts, but it is especially well exhibited in many orchids and mints where a huge lip has developed at the expense of the

stamens and usually the other petals also. Use and disuse go hand in hand as a necessary corollary of the law of conservation, and no flower escapes their operation. The use of a part gives it the advantage in securing an adequate supply of material and energy and is the decisive fact in determining that some other part will now receive less than its share and will consequently dwindle or even disappear. Active use always constitutes a better claim than passive possession and it takes the right-of-way in all emergencies that confront the plant.

DIVISION OF LABOR AND PARENTAL CARE

Two signal advantages follow from the greater use of one part, such as the corolla, or of certain petals, as in a landing platform. The first of these is a division of labor, in accordance with which each part has its own tasks and hence does them more efficiently than when all the parts do the same work. A bee may land on any petal of a geranium and secure the nectar without touching either anther or stigma. On the contrary, it always alights on the lower lip of the sage, assumes the same position at each flower and regularly touches anthers and stigma in turn as it sips the nectar. In addition, pollen, stigmas and nectar are exposed to dew and rain in the geranium and most regular flowers, while they are protected by the upper lip in the sage and most other irregular ones. A remarkable division of labor occurs in many wind flowers, in consequence of which some individuals produce only stamens and others only pistils, as in the cottonwood and box-elder. Each blossom does its work better by virtue of having only one main task to perform, and this is especially significant in the case of the pistillate flower, which can now devote more energy and material to the care of the young plant in the seed. Such an increase of parental care is the regular outcome of use and disuse and of division of labor, and is characteristic of the more efficient or higher flowers, such as asters, grasses, walnuts, etc. It is expressed most often by producing but a single seed in each flower and providing the young plant with a larger store of food against the day of germination. It also takes the form of greater protection in

other ways and particularly in the devices that permit the seeds to find new homes, such as hooks, spines, cotton, and parachutes like that of the dandelion. The outcome of all such changes is termed specialization or advancement and results in the production of so-called higher forms of flowers from lower ones.

CHANGES OF FLOWER PARTS

It is both interesting and helpful to know that just as all flowers are made of but four parts or less, so the changes that these undergo in becoming more efficient and hence specialized, fall under four heads. In glancing at a hundred unlike flowers, one might well feel that they exhibited as many changes, but in fact these are only different expressions of four basic modifications, namely, changes in number, relation, position, and shape.

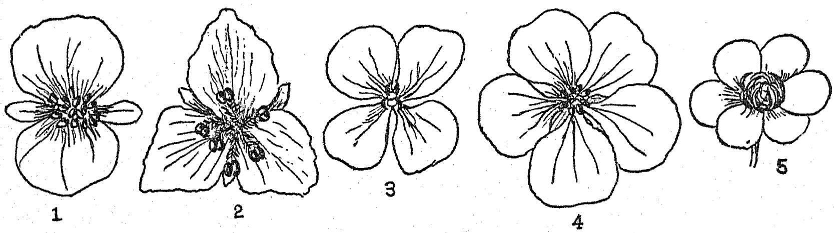

Fig. 41. Number-plans of Flowers
(1) Begonia; (2) Spiderwort; (3) Wallflower; (4) Geranium; (5) Creamcups

The number plan of the flower often runs through all four parts, but as flowers become more specialized, it first disappears in the pistils and then in the stamens. It persists almost universally in the corolla and calyx, often when these have been greatly reduced in response to wind pollination. The disuse of a part may ultimately lead to its complete disappearance, as in the case of the corolla of most wind-pollinated flowers, while a used part never vanishes entirely, though it may be reduced to one, as is true of the stamens in practically all orchids.

UNION OF PISTILS

Changes in relation are concerned with the union of parts. In the simpler flowers such as buttercups and roses, the four

parts are not only separate, but the members of each part are separate from each other. Mallows have made one of the first experiments in union by combining a number of pistils into a ring, forming a compound pistil, but their original nature is shown by their splitting when ripe into the "cheeses" of childhood days. The very task of making a thousand pistils for the flower of a mouse-tail means that may of these will be poorly made, while that of getting so many separate stigmas pollinated is beyond the ingenuity of the blossom or the industry of the

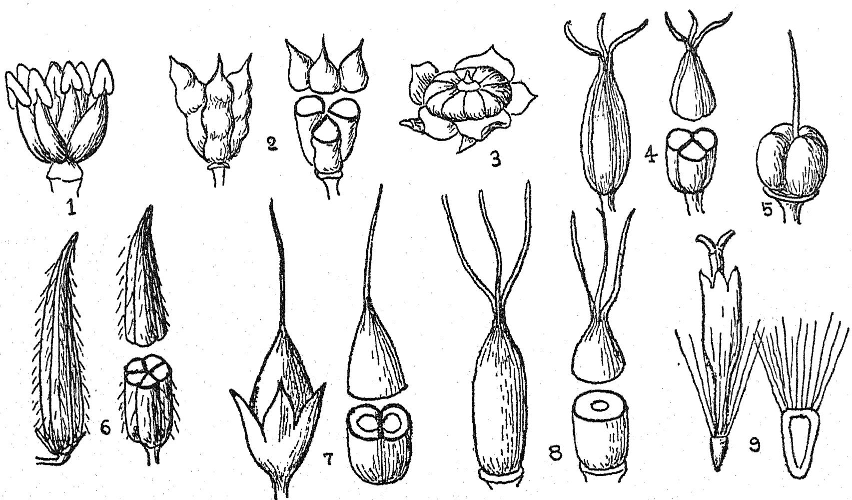

FIG. 42. SIMPLE AND COMPOUND PISTILS
(1) Meadow-rue; (2) Monkshood; (3) Mallow; (4) Wand-lily; (5) Bugle; (6) Yellow Oxalis; (7) Pentstemon; (8) Catchfly; (9) Senecio

bee. The laws of conservation and of use and disuse step in, with the consequence that the number of pistils is steadily reduced. Even in the genus *Ranunculus*, the true buttercups, the pistils have decreased from several hundred to a score or less, while in the more efficient larkspur and monkshood the number is but two or three.

The next advance consisted in uniting the few simple pistils into a compound one and carried with it two great advantages. The first was a saving of material and greater stability, much as

man has achieved by building one house of several rooms instead of several of one room each. The second was a great increase in the certainty of pollination, due to bringing all the stigmas close together or combining them into a single one that would be readily dusted by the insect visitor. Once secured, these gains were so decisive that all flowers thereafter possess compound pistils, in which the original number of simple pistils is revealed only in the number of stigmas, its lobes or the partitions of the ovary.

UNION OF PETALS

The union of the separate petals into a bell-like or tubular corolla has had similar advantages. It not only saves material

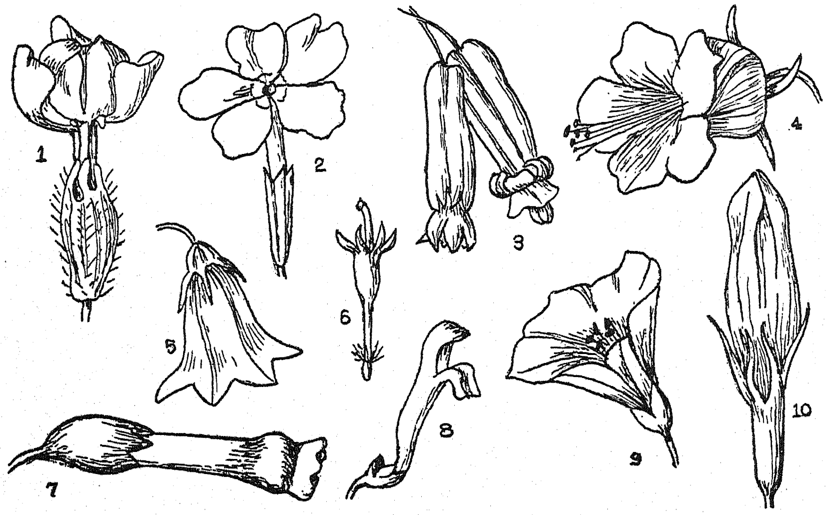

Fig. 43. Union of Petals and Sepals
(1) Catchfly; (2) Verbena; (3) Firecracker-flower; (4) Bell Phacelia; (5) Bluebell; (6) Bachelors-button; (7) Tree-tobacco; (8) Skullcap; (9) Bindweed; (10) Closed Gentian

in most cases, but it renders the color mass more conspicuous, facilitates the search for nectar and also often serves to protect this as well as the anthers and stigmas. Again, as in the case of united pistils, the improvement in efficiency is so great that this advance has persisted after it once appeared. The gain is

less clear in the case of the sepals, but the economy in material and the increased protection seem to explain why union in the corolla has practically always been accompanied by a similar change in the calyx. Union of the stamens is less advantageous and is consequently infrequent. In the hollyhock and its relatives, the union of the filaments brings the anthers into a better arrangement for rapid loading and this is more or less true of the same device elsewhere. The most obvious advantage is found in the tiny flowers of asters, dandelions and other composites, where the filaments are combined into a narrow tube of great significance in the peculiar pollination of these plants (Fig. 60).

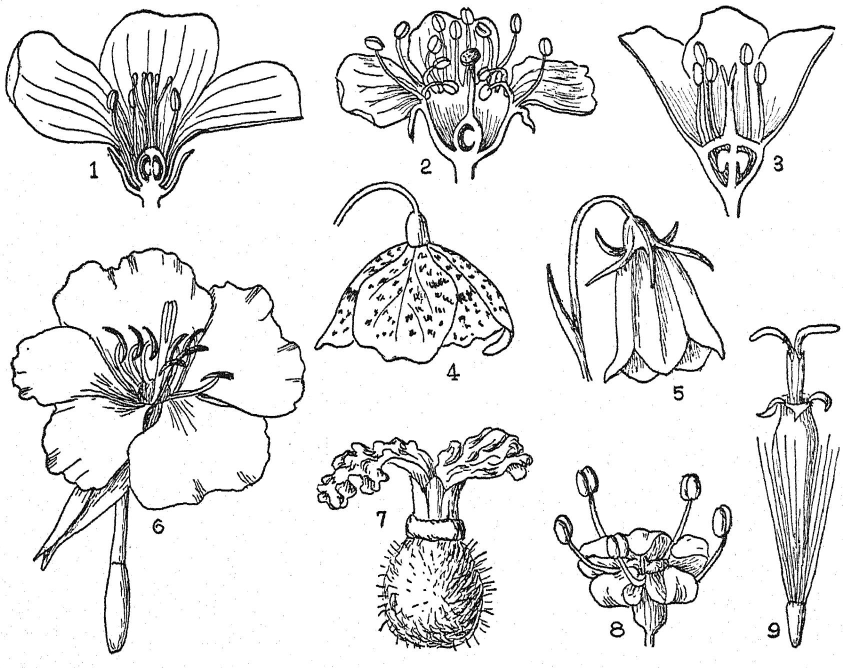

FIG. 44. ELEVATION OF THE COROLLA

(1) Long-section of Flax flower with ovary attached above the other parts; (2) Section of Cherry-blossom with stamens and petals above ovary; (3) Section of Mock-orange with ovary below the other parts; (4-9) Types of flowers with corolla completely raised above ovary; (4) Hydrotænia; (5) Bellflower; (6) Evening-primrose; (7) Walnut (corolla lacking); (8) Fennel; (9) Senecio

CHANGES IN POSITION AND FORM

Changes in position operate almost wholly in placing the corolla or stamens on a higher level with respect to the other parts of the flower. It is less important in the case of the stamens, where it usually results from the union of the petals and the fusion of more or less of the filament with the corolla tube. It regularly results in putting the anthers in a more convenient position with respect to loading. The elevation of the corolla is much more significant, since it decreases the masking of the color by the calyx or other parts and correspondingly increases its attraction for pollinators. This slight difference would seem to be insignificant, but it actually has much value, as can be shown by experiment. Bees in particular fly in a "bee-line" and hence are guided in large measure by the lateral expanse of color in a flower. If this be covered with green leaves, the flower is visited little or not at all, in spite of the color as seen from above. The significance of elevation is further indicated by the fact that it regularly persists in those lines of evolution in which it first appeared. Flowers with an elevated corolla are usually termed epigynous, i. e., upon the ovary, or the ovary is said to be inferior, as in the iris and the honeysuckle, for example.

As long as the petals do the same work in the same way, they are alike in shape and position, and the flower is said to be regular. When one or more petals are turned into a landing platform or fashioned into a sack or spur for nectar, so that they become unlike the others, the flower is irregular. If the calyx is colored, it may experience a similar change, resulting in the very irregular blossom of the larkspur and monkshood or the spurred one of the garden nasturtium. It is this change that produces the most striking differences in flowers and at the same time gives a curious likeness to some that are totally unrelated. A hasty glance at a monkshood, sweet-pea, violet, orchid, and snapdragon might well lead the beginner to think them closely related, though as a matter of fact they belong to more or less widely separated orders. The advantages of the irregular form

with respect to landing, guidance, rapidity of visits and protection of nectar and pollen are obvious, and hence this advance is characteristic of all the highest insect-pollinated flowers. It is not confined to them, however, as the lowest group of all, the buttercups, have tried this experiment successfully in the columbine, larkspur, and monkshood, and the geraniums likewise in

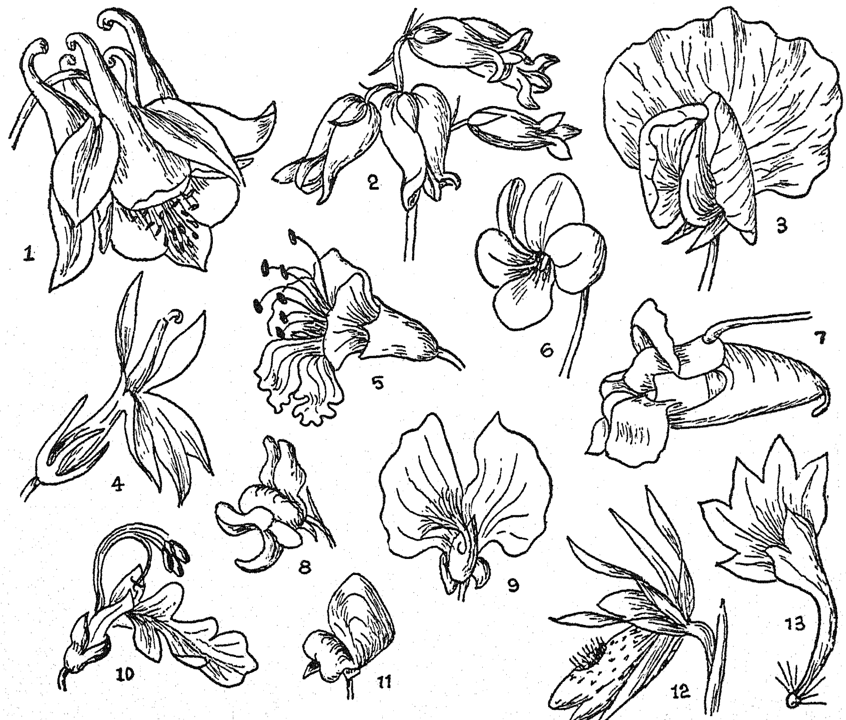

FIG. 45. TYPES OF IRREGULAR FLOWERS
(1) Columbine, buttercup family; (2) Pink Dicentra, fumitory family; (3) Sweet-pea, pea family; (4) Cardinal-flower, lobelia family; (5) Horse-chestnut, maple family; (6) Pansy-violet, violet family; (7) Touch-me-not, geranium family; (8) Bladderwort, bladderwort family; (9) Polygala, polygala family; (10) Teucrium, mint family; (11) Slipperwort, snapdragon family; (12) Calypso, orchid family; (13) Bachelors-button, aster family

the touch-me-not and the nasturtium. While insects have doubtless had much to do with the development and perhaps the origin

of such forms, some of the simpler ones can be produced experimentally by changing the relation of the flower to the pull of gravity.

While the structure of the flower itself is not changed, its appearance is often transformed by the presence of the so-called floral leaves or bracts found in the cluster. These are often so conspicuous or so closely associated with the flower as to be taken for a part of the latter or even for the entire blossom itself. This is what occurs in the calla "lily" and the jack-in-the-pulpit, where the brightly colored part is really a leaf folded around the tiny flowers. The real character of such leaves is more clearly revealed in the poinsettia, but is again obscure in the flowering dogwood, where the bracts look exactly like petals. In the paintbrush the real flowers are more or less visible, but the brilliant color is due entirely to the bracts. In both the asters and the grasses, the bracts are often mistaken for parts of a flower, so intimately have they been worked into the cluster.

The efficiency of a working flower is determined by its success in securing the best type of pollination and producing the best kind of seeds. In both these respects its success can be measured with more or less accuracy, but this is a difficult task, open only to the investigator. For all others the most satisfactory test of efficiency is noting the changes that the flower has undergone in conserving its energy and material, dividing up its tasks among the various parts, and increasing the care given its offspring, which are the plantlets in the seeds. By this test, the least efficient flowers would be those with a large number of each part, separate pistils and separate petals, corolla not elevated and regular petals. Such are the features of the buttercup and magnolia flowers, and in consequence the buttercup order is regarded as the earliest and lowest of all the flowering plants. Such flowers are also spoken of as the simplest or least specialized. They are regarded as the ancestors of all other flowers, which have developed from them in accordance with the changes discussed above.

EVOLUTION AND RELATIONSHIP OF FLOWERS

Rôle of the Flower Chart

THE flower chart tells the story of how some of the simplest and least efficient buttercups did their work of pollination and seed production better and better under the stress of changing conditions. In the course of time some developed into geraniums, roses, and lilies, and these in their turn gave rise

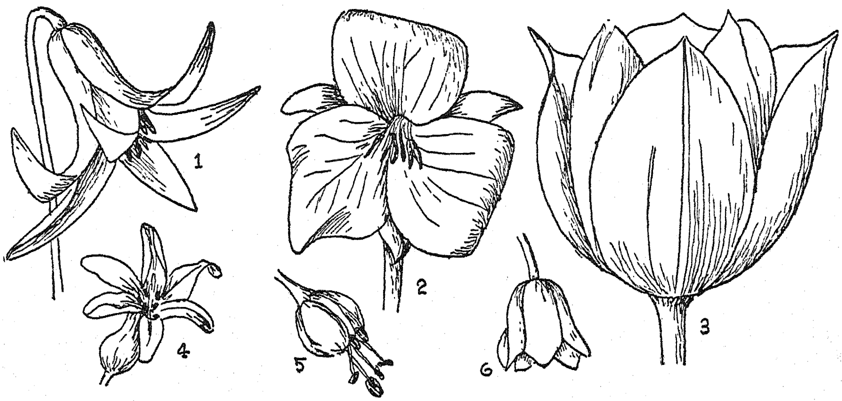

Fig. 46. Genera of the Lily Family
(1) Spring-lily; (2) Trillium; (3) Tulip; (4) Hyacinth; (5) Nodding Onion; (6) Asparagus

to all the higher and more efficient flowers of field, forest and garden. The chart consequently furnishes a comprehensive yet detailed picture of the evolution and relationship of flowering plants, in terms of efficiency in daily work as well as in the meeting of emergencies. The upward journey of buttercups in the remote past resembles such a journey as one might make today. It had a starting point, passed through a great center, and finally came to an end, at least for the immediate present. The buttercups represent the beginning, the great centers are the geraniums, roses, and lilies, and the corresponding stopping places are mints and goosefoots, asters and walnuts, orchids and

grasses. In consequence, by far the best plan to bring the chart into simple order is to see it at first as consisting only of these outstanding groups, which are to be connected with each other by the details of their progress, as is done in the skeleton key on page 93.

An understanding of the mechanical details of the chart also aids greatly in revealing its essential simplicity. The flowers and their names may be taken for granted, except that it must be kept in mind that each name may be used in three senses, though these are closely related. "Lilies" may refer to the actual *species* of the genus, to the *family* that contains them as

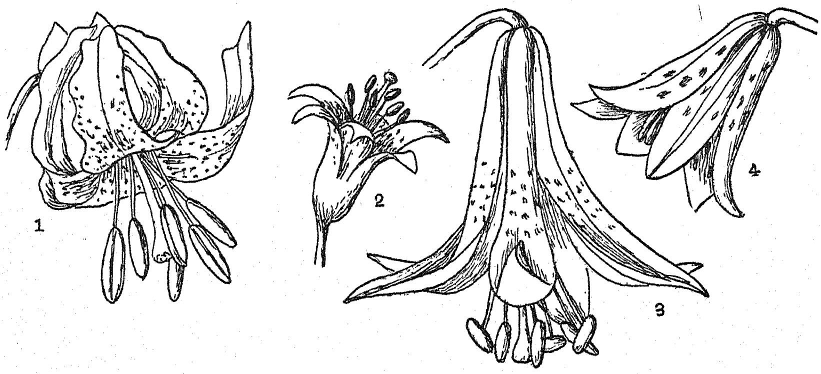

FIG. 47. SPECIES OF THE LILY GENUS
(1) Chaparral Lily; (2) Fairy Lily; (3) Yellow Lily; (4) Thimble Lily

well as the related genera, trillium, tulip, etc., or to the *order* consisting of related families such as the lily, spiderwort, smilax, and others. On the chart all the names refer to orders, with the exception of a few such as the peas, which form a family belonging to the rose order. The black lines that lead from the buttercups through the three centers to end in the six highest groups are lines of descent, and hence of evolution and consequent relationship. The solid ones indicate that the progress in efficiency has been made under the direction of insect pollination, and the broken lines that the changes have been worked out under pollination by the wind. Each line is a path of descent and this means that each group consists of lineal descendents

of the preceding one, while those of two adjacent lines, such as mints and goosefoots, are only very distantly related through their common descent from geraniums. The color lines that cross the black ones mark the point at which each progressive advance in efficiency occurs, and in addition emphasize the fact that this happens at very different levels in the lines of descent.

The air of mystery enveloping the formula for each order or flower type vanishes as soon as one realizes that the four main abbreviations, *Ca, Co, S, P,* stand for calyx, corolla, stamens and pistil (Figs. 52, 55, 57). In short, the formula is merely a graphic way of revealing the structural features of a representative flower. It is based upon the four flower parts and the four changes that these regularly undergo, namely, union of pistils and of petals, elevation of corolla, and change in the shape of the petals. The number of members in each part is shown by an exponent; the sign ∞ is employed for a large number, usually 20 or more, and x for a smaller variable one. The hyphen denotes variation and when used with the numbers reversed, e.g., 4-2, indicates the advance in reduction within the order.

Union is indicated by a circle around the exponent and partial union by a semi-circle. When stamens are united by their filaments alone, the semi-circle is placed below the number; if the anthers are fused, it is put above. A broken circle denotes the condition often found in the pistils of mallows, when the fusion is so incomplete that they separate when ripe. In the united or compound pistil, the exponent indicates both the original number of simple pistils and the number of seed-chambers or "cells" now present. In the earlier examples of union, such as the lily and geranium, there are as many cells as there were simple pistils, but in the highest types the partitions have disappeared, leaving only a single cell. In such cases the first exponent of the pistil gives the original number of simple pistils or carpels, and the second the number of cells, which is usually one. The elevation of the corolla is shown by a horizontal line above the pistil and that of the stamens by a similar line above the corolla. An irregular corolla is designated by means of the + sign, with the sequence reversed, e.g., 3+2, while the sequence in the calyx

is usually the opposite, 2+3. A similar method is employed for the irregular grouping of stamens, such as 9+1 in the peas, and for such exceptional modification of the carpels as is found in the grasses. Finally, when the calyx becomes bright-colored and works with the corolla in attraction, the two are joined by a tie, as is seen in the formula for the lilies. The separation of stamens and pistil in two different flowers is indicated by $\cancel{m}$ between S and P when the species is monoecious and $\cancel{d}$ when it is dioecious.

The cross-lines denoting the steps in advance are all in color, and the same color is often carried in the formula for the part affected, as well as in the name of the change itself. In addition, there are three such lines for changes in number and grouping that are not indicated in the formula, in order to make them more comparable and to save complexity. The line of diclinism marks the separation of the stamens and pistils in different flowers, as in the walnuts and oaks where they are on the same tree and in the poplars and box-elders which have them on different trees. The flower regularly produces several to many seeds in each fruit in the orders below the line marked "single seed" and a one-seeded fruit above this line. Finally, the grouping of a number of flowers into a definite cluster or community, as in the head of the sunflower and the spikelet of the bluegrass, is indicated by the line for social flowers.

Buttercups and Their Experiments

It is as interesting as it is significant to find that the buttercup order has developed more different kinds of flowers than any other. This is an indication of its progressive nature as shown by the ability to adjust the flower to a wide range of experiences, and it is this adaptability that renders buttercups today exceedingly favorable material for experimental studies of evolution. Buttercups have undergone nearly every important change that marks the advance of the higher flowers, but such experiments were local and did not give rise to the lines leading to the three great centers. This fact supports the view that specialization limits adaptability to a narrow field and serves to explain why

the lines of descent have sprung from the more primitive buttercups rather than from the specialized larkspurs and meadow-rues. The buttercups thus forecast the evolution of flowers to a remarkable degree, and this fact was taken advantage of by Jussieu more than a century ago, when he derived from this order the principles upon which he founded the first natural system of flowering plants.

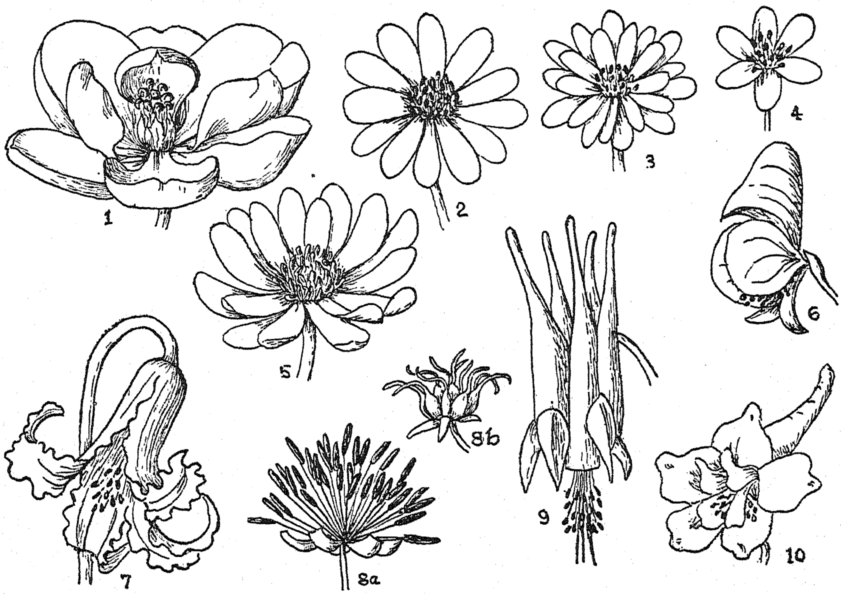

FIG. 48. FLOWERS OF THE BUTTERCUP ORDER
(1) Magnolia; (2) Buttercup; (3) Windflower; (4) Hepatica; (5) Marsh-marigold; (6) Monkshood; (7) Viorna; (8) Meadow-rue; (9) Red Columbine; (10) Blue Larkspur

The most primitive and hence the earliest of all true flowers are those of the magnolia, calycanthus, and the buttercups proper or crowfoots (*Ranunculus*). They may consist of a dozen or more sepals and petals and of a large number of stamens and pistils, frequently more than a hundred each. In the large majority of the buttercups, the number of sepals and petals has been reduced to less than ten, but without a corresponding decrease in the stamens and pistils. The calyx and corolla also exhibit a general tendency toward what later become the pre-

ferred number plans for the flower, namely, 3, 4, and 5. Great uncertainty still exists as to the best plan, however, and all possible numbers from 2 to 10 have been tried out by different genera. The four flower parts have behaved very unequally in this respect, and it is not unusual to find the sepals reduced to 3-7 and the petals numerous, or the stamens many and the pistils few, and so forth. Moreover, in some of the most familiar flowers

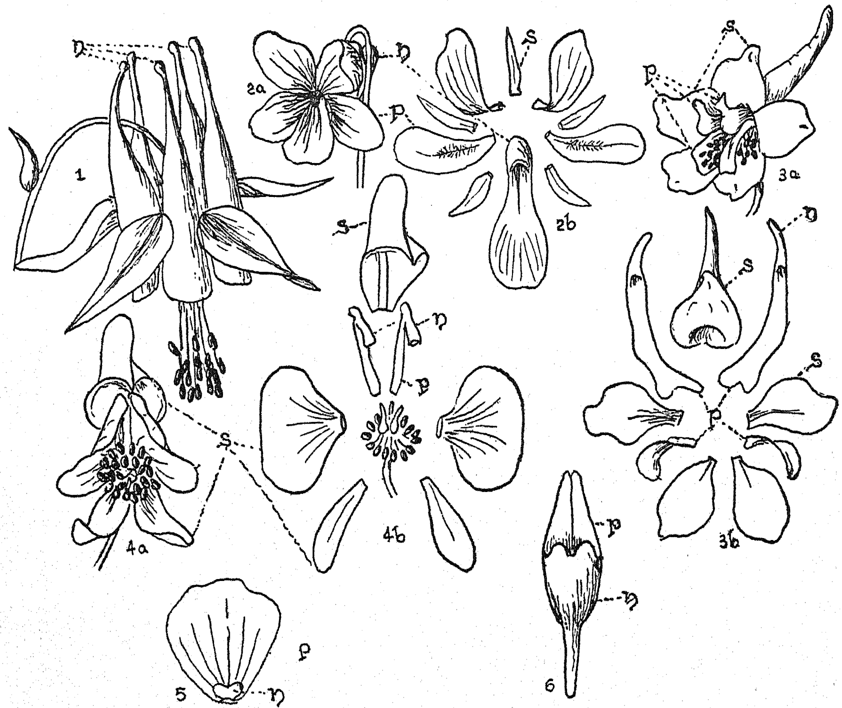

FIG. 49. TYPES OF NECTARIES
(n, nectary; p, petal; s, sepal)
(1) Columbine; (2) Violet; (3) Larkspur; (4) Monkshood; (5) Buttercup; (6) Eranthis

of this group, such as the anemone, hepatica, clematis, and marsh-marigold, there is no differentiation of sepals and petals and the latter are commonly regarded as lacking.

The problems of pollination have led to many experiments in the endeavor to increase the efficiency of the nectary. Flowers

with sepals alone lack nectaries, and a few of those with petals also. As a rule, however, each petal contains a pit or scale that serves as a simple nectary, while in others the petal itself is modified into such an organ. In the columbine the lower part of each petal becomes a long nectar-bearing spur, and in the globe-flower the entire petal is changed into a tiny nectary. The two petals of the monkshood and two of the four of the larkspur have been turned into long narrow tubes for collecting nectar and are then tucked away for protection in a spurred or hooded sepal. With this has gone the further specialization of the calyx by which it not only does the attracting but also takes care of landing and guidance. This has had the interesting consequence of making such flowers resemble much higher ones, but their true relationship to the buttercups is shown by the separate pistils and many stamens. The most striking advance made by buttercups is shown in the meadow-rue, in which the stamens and pistils are not merely in different flowers but also on separate plants, i.e., dioecious. Finally, in the maid-in-the-mist, the five ovaries are united into a pod, while in the baneberry, the pistils have been reduced to a single one, again suggesting the advances that mark higher types of flowers.

Ancestral Lines from Buttercups to Lilies

Although this change took place long before man appeared on the earth and its exact stages can never be absolutely known, there is so much evidence of the probable steps in advance as to warrant a feeling of security in regard to them. In spite of the shifting number plan among the buttercups, the larger number of them must have long ago settled upon a plan of 3 or 5. The plan of 3 is typical of the magnolias and suggests that it became fixed earlier than that of 5. In any event it came to be the regular number for sepals and petals in the line of descent that led to the lilies. With this fixation of the number plan went striking changes in the plant body, of which the presence of one instead of two seed-leaves or cotyledons has served to give the name monocotyledons to this great group. (Frontispiece.)

The flower of an arrowhead is essentially that of a buttercup with the calyx and the corolla in 3's. It does not constitute an advance upon the buttercup type, but is merely one of the variations of it. The arrowheads are in further agreement with the ancestral buttercups, beginning with a large number of stamens and pistils in each flower and gradually reducing these to 12, 6, or even 3, in accordance with the law of conservation. The common arrowhead of our ponds and streams resembles the meadow-rue among buttercups to the extent that the stamens and pistils are in separate flowers. In some members of the order the pistils are reduced to three and in others they are more or less united and the ovules numerous, a condition which approaches the structure of the lily flower very closely. When all three of these changes occurred in the same flower, the latter became the representative of a new order, the lilies. Such a flower is the common spiderwort with green calyx and purple corolla in 3's, 6 stamens and 3 pistils united into a compound one. Thus, the one great advance is represented by the saving of material and the increased certainty of pollination arising from this fusion. The wake-robin or trillium exhibits the same essential structure as the spiderwort, but the great majority of members of the lily family have undergone a further change. This consists in coloring the calyx like the corolla to increase the attractive surface and explains why the lilies are among the most beautiful of flowers. From the standpoint of pollination, the desirability of this change is indicated by comparing the spiderwort or wake-robin with the geranium and rose. The petals make a much more complete circle of color in the latter, an advantage usually to be gained under the number plan of 3 only by calling the sepals to the aid of the petals. This advance had far-reaching consequences, as we shall see in tracing the further progress of lilies and their descendants.

Buttercups and Roses

Buttercup flowers are so much like the simplest ones of the rose family that the beginner will find no real difference between them. The line of descent is unbroken and the two families

must be distinguished on the basis of general appearance rather than upon an obvious character. The rose, apple and related flowers have developed a definite calyx cup, which serves to place the corolla and stamens in a more elevated position. The tendency toward this change is already felt in the cinq-foils and their relatives and hence aids in distinguishing them from buttercups. In the latter the parts are all placed separately on the tip of each flower stalk or receptacle and can be pulled off independently, while in the simplest roses the petals and stamens are inserted on the calyx and are torn off with it. The rose order resembles the buttercups also in the large number of experiments that the flowers have made, though it is set off by the many kinds of fleshy fruits developed for securing the distribution of seeds.

Ancestral Lines from Buttercups to Geraniums

The pathway taken by the buttercups that finally changed into geraniums is less definite than those that led to roses and lilies. This is largely the result of much more active evolution in this region, with the consequence that the line of descent is more broken by diverging groups. Both the poppies and the mallows appear to have sprung directly from the buttercups, as shown by their general structure, but especially by the numerous stamens, and the separate simple pistils of a few primitive genera. However, the poppies are not on the main line of development, as the pistil early became compound and 1-celled, and they terminate in the mustards, with characteristic pod and stamens. The simplest mallows bear numerous simple pistils, but in most of our common species these are reduced to 10 or 5 and grouped in a ring. In the so-called "cheeses," the pistils separate as the fruit ripens, thus suggesting that the union is recent and incomplete. The mallows proper are peculiar in having the stamens united by their filaments into a massive column, but the closely related flowers of the linden bear them in five loose groups, approaching the condition found in the true geraniums.

The further reduction of the stamens to 15 and the pistils

to 5 gives rise to the flower of the geranium order, in which the mallow ancestry is still indicated by the union of the stamens and the separation of the pistils when ripe. The law of conservation and of use and disuse is further wrought out in this group, as is shown in detail in its further evolution.

Comparison of the Three Great Centers

The lilies, roses and geraniums are alike in having sprung from the buttercups and given rise to lines of descent that have followed the same general course to end in the highest types of flowers. The pathway in each is short and definite and ends at much the same stage of progress. In spite of their characteristic differences, the lily, geranium and rose are essentially alike with respect to pollination. They are large flowers with a complete disk of color, and possess very nearly the same efficiency in attraction. The spiderwort and geranium differ little but in the number plan, the stamens and pistils having reached exactly the same stage of advance while the lily has approached the geranium even more closely in one respect by coloring the sepals to complete the attractive disk. The rose departs more widely inasmuch as it retains its many stamens and separate pistils and develops a cup-like calyx, but these differences largely disappear in other members of the family. It is interesting to reflect that such differences are due to the varying solutions worked out by progressive buttercups and that the same solution of their pollination problems would have given one great center instead of three.

Each of the three orders contains a very large number of genera and species, and has tried out many experiments in the endeavor to achieve more efficient pollination and seed-production. The great majority of these have ended blindly, at least as we see them today, but two of them have given rise to long lines of descent in the case of each center, while the roses have also produced a third shorter line. In each case one of these lines has been developed under the stimulus of insect-pollination and the other under that of wind-pollination. This has given to the chart its characteristic form, namely, two related but diverg-

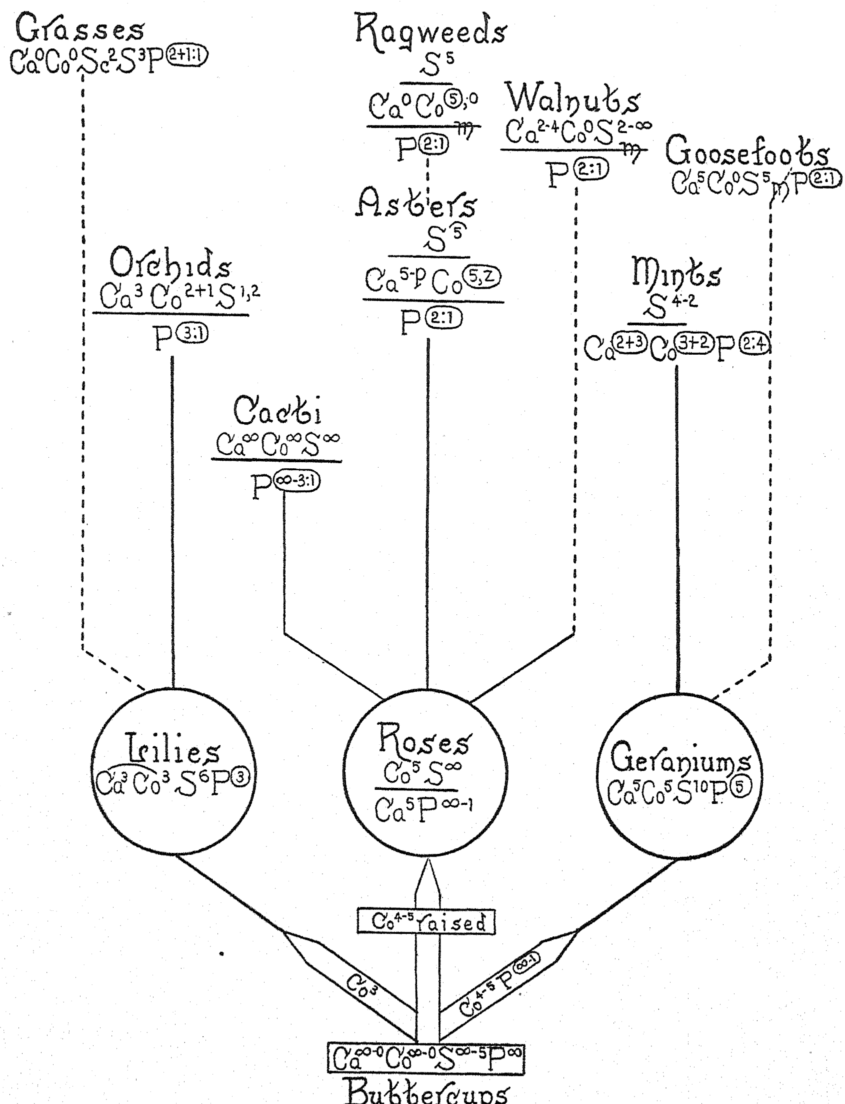

FIG. 50. SKELETON KEY TO THE FLOWERING PLANTS

ing lines of evolution from each of the three centers, ending in six highly specialized groups which represent the highest levels that the evolution of plants has reached. It is interesting to note that while the flowers of each pair of lines are related to each other by descent from a common center, those of the three insect or three wind-pollinated lines superficially resemble each other much more closely, in spite of their more remote relationship. This is due to the fact that the corolla shows the most striking response to the method of pollination.

Geraniums and Their Experiments

The geraniums show their descent from the mallows and lindens by the several rows or groups of stamens and also by the separation of the pistils when ripe, in the wild geraniums and their close relatives. The number of stamen rows is usually two, but the constant tendency toward reduction is exhibited

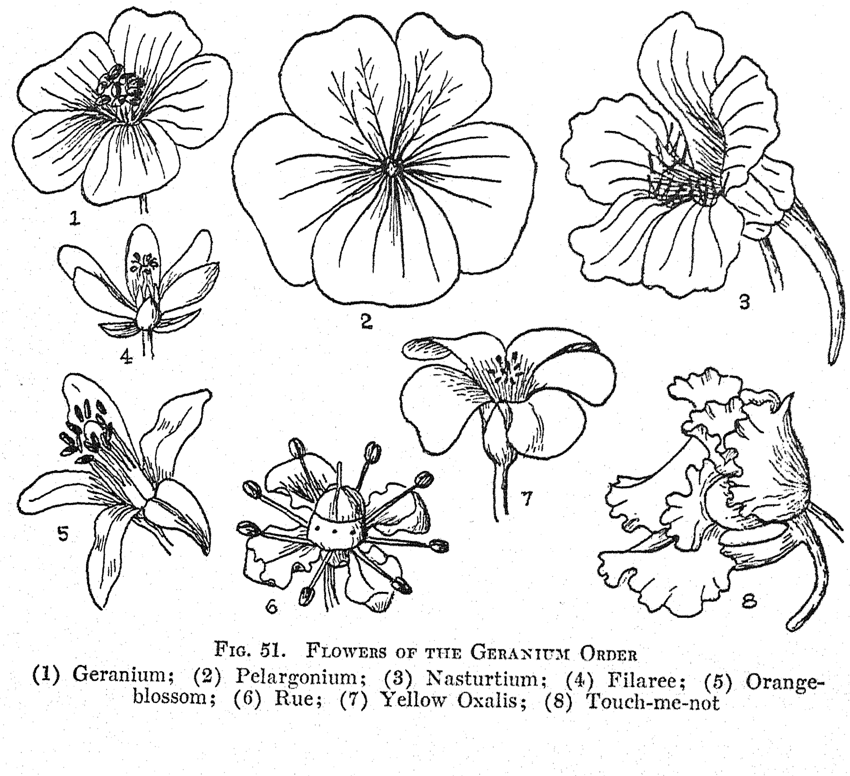

Fig. 51. Flowers of the Geranium Order
(1) Geranium; (2) Pelargonium; (3) Nasturtium; (4) Filaree; (5) Orange-blossom; (6) Rue; (7) Yellow Oxalis; (8) Touch-me-not

by the alfilaria, or "filaree," which possesses five perfect and five antherless ones. The pistil consists of five parts as a rule, and the ovary is consequently 5-celled, but cells may be either more numerous in the oranges or less so in the rues. The corolla and calyx have changed much more, so much in fact that the touch-me-not gives little hint of its relationship to the geranium. At first glance the difference appears so great as to warrant placing this in a separate family of its own, but a careful scrutiny indicates that a family relationship exists between the two.

The flowers of the wild geranium are regular and the calyx is green, while in the cultivated "geranium" or pelargonium there is a marked tendency to become irregular. In the rose and ivy geraniums, the two upper petals have changed their position and markings, and often their shape as well, and in some cases one of the sepals has become more or less sack-like. This change has been carried much further in the nasturtium to produce a long spur-like nectary, and at the same time the calyx has assumed something of the bright color of the corolla. The three lower petals have developed both claw and beard, while the two upper ones have fused with the sepals and are striped like them to help form a guide to the nectary. The touch-me-nots have transformed the spurred sepal into a large cornucopia at the expense of the other four, all of which are small and two of which may be wanting. The petals are free and more or less alike in the simpler forms and the forward one is much larger than the others which it encloses.

The step from geranium to the sheep sorrel or oxalis is but a short one, the most important difference residing in the fruit. Instead of being beaked and separating at maturity to scatter the single seeds, it is a capsule that splits along the ridges to free the many seeds. A further change in the ovary by which the partitions begin to disappear between the cells leads from oxalis to the pink family with its numerous progeny.

Geranium-Mint Line of Descent

The further improvement of the geranium stock is foreshadowed by their close relatives, the rues. The irregular corolla

of the dittany suggests that of the pelargonium, and certain other flowers have begun to unite the petals into a tube. This advance leads directly to the heaths, in which all stages of fusion may be seen, from the free petals of the pirolas to the perfect bells of blueberry and heather. The ancestral traits of the geraniums still persist in the double ring of stamens and in the cells and lobing of the ovary. The flower in the heaths has been specialized in a number of ways, but we are interested at present only in the changes that have led to the phloxes and morning glories. These are best represented by the flowers of the mountain laurel and by those of azalea and rhododendron. In these especially, the petals are united only toward the base or they may be entirely free. In some cases the stamens are undergoing a further reduction to five and the pistil is already 4-celled, both of which are features to be found in the phlox order. There is in consequence no real gap between heaths and phloxes, though, as in many cases, it is impossible to discover a particular heath that may be the direct ancestor of one of the phlox family.

PHLOXES

The phloxes are one of the most important orders of flowering plants, not only because of their large number and the many species in cultivation, but also on account of the new lines of descent that have sprung from them. The simplest flowers are probably those of the phlox family proper, in which the 5-celled pistil of the heaths still shows occasionally, although most of our common species, such as the sweet william and gilia, exhibit but three cells. The transition to the morning glory family is a simple one, consisting chiefly in the reduction of the ovary to two cells, while minor changes of interest are represented by the ephemeral flowers and the twining habit of the stem. The potato family differs from the morning glories in producing many-seeded fruits, often with fleshy pulp, such as the tomato, nightshade and eggplant. The line between the forget-me-not or borage family and the morning glories is a shadowy one, some of the wild heliotropes resembling the latter much more closely than they do their borage relatives. In most of the latter, how-

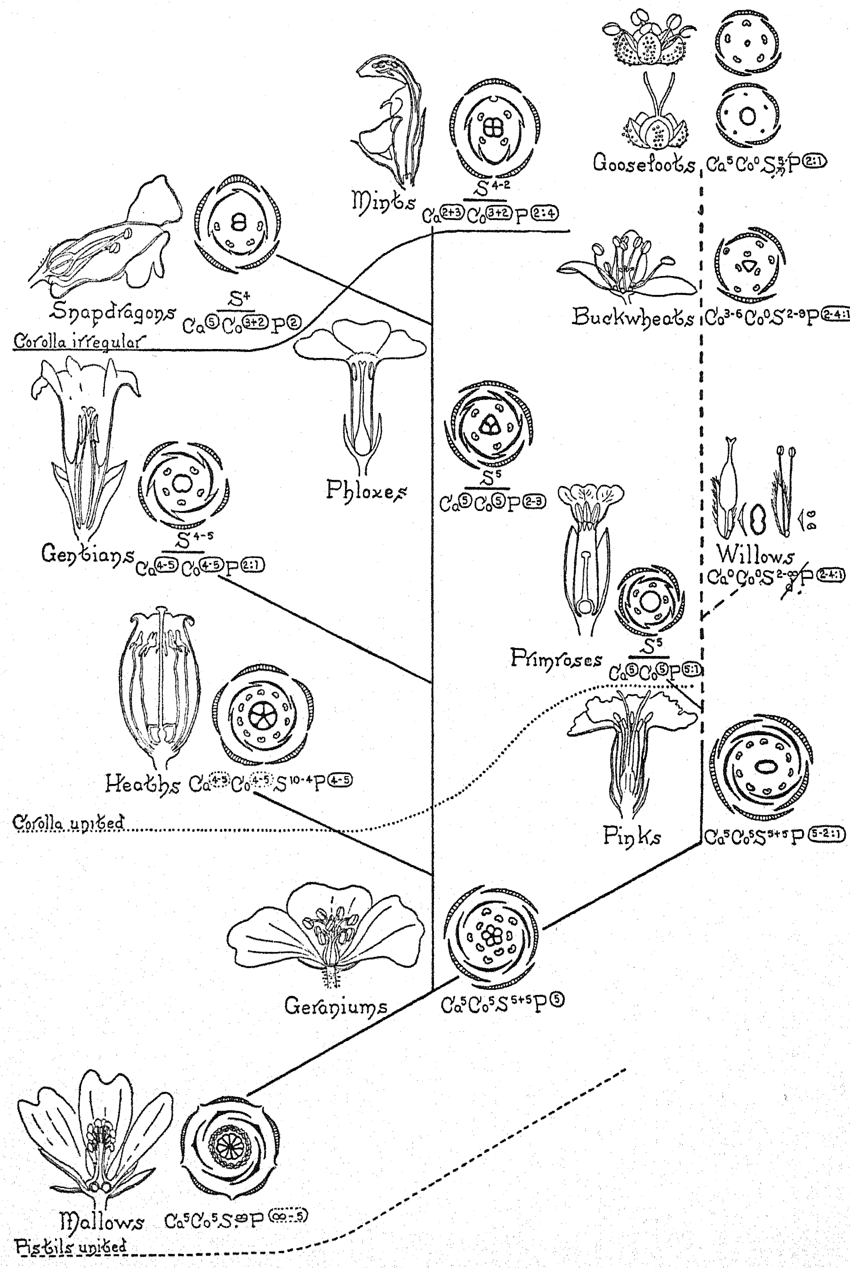

FIG. 52. INSECT AND WIND POLLINATED LINES OF DESCENT FROM GERANIUMS

ever, the 2-celled ovary is again divided to form four 1-seeded nutlets, often with barbed prickles as in the sticktights. The highest of these are in the process of becoming irregular and thus look forward to the more advanced verbenas and mints. The waterleafs and blue-eyes have reduced the ovary to a single cell in some cases, but their relationship to the phloxes is still indicated by the frequent occurrence of an incomplete cross-wall. The dodders are curious twining parasites, covering coarse weeds and even cultivated plants with a web of creamy or yellow threads. Their leaves are gone, but the tiny flowers show that these are only morning glories that have found it easier to steal their food than to make it (Fig. 64).

GENTIANS AND MILKWEEDS

The gentians are so closely related to the phloxes that they might well be included in the same order, the one technical difference of leaf position permitting a number of exceptions. However they have undergone a much more varied evolution, resulting in such highly specialized flowers as the milkweed and the ash. The gentian family itself is closely related to the morning glories and the potatoes, and differs chiefly in the reduction of the ovary to a single cell, though often with a trace of a second one. The loganias are even more closely connected with these two families, the ovary being completely two to four-celled. From loganias have sprung the apocynums, including the dogbanes, periwinkles and oleanders, in which the two cells of the ovary have usually turned into separate pods, such as are seen in the milkweed. The first glance at a milkweed flower is bewildering, for it seems very unlike its relatives. The stamens are united into a column to which are attached five hoods, often provided with horns, both of which are entirely novel features. In addition, the pollen is packed into two masses connected by a sticky band which adheres to the head of the visiting insect, giving it the appearance of two horns.

In spite of these striking changes, the milkweeds still exhibit the steps by which they have evolved from the dogbanes. The latter possess a milky juice and a fruit consisting of two separate

pods, both features that are typical of milkweeds. In the simplest of the milkweeds the filaments are distinct or nearly so, as with the dogbanes, but in most they are coherent or united into a tube. The next step in advance is the development of an appendage on each filament, which takes the form of an inverted cap in our common milkweeds, making their characteristic crown. In some genera this crown may become double or even triple. Finally, in the true milkweeds of the genus *Asclepias,* so common in grain-fields and along roadsides, a crest or horn develops inside the cap. Such a crested crown is usually the most conspicuous feature of the flower, the less showy corolla being reflexed and hiding the calyx.

The olive family, containing the olive, privet, lilac and ash, is interesting because it furnishes a complete record of the changes that insect flowers experience in response to wind-pollination. The common ashes are the result of a thorough-going response to wind, in which the calyx and corolla have completely disappeared and the stamens and pistils are on different trees. Even the fruit has felt this influence, as it has changed from a pod such as that of the lilac to a winged one resembling that of the maple. However, some species of ash still have all four parts in the same flower, as in their near relatives, the lilacs.

SNAPDRAGONS, BORAGES AND MINTS

The potato family passes so gradually into the snapdragons that it is almost impossible to draw a line between them. Some of the potatoes have irregular corollas, while a few of the snapdragons possess regular ones; the former nearly always have five stamens, the latter four or two, but occasionally the fifth persists as a remnant. The mulleins might well be placed in either group, since the corolla is nearly regular and the stamens are five in number. The foxgloves, pentstemons and monkey-flowers are representative members of the snapdragon family, while the butter-and-eggs, snapdragon and calceolaria are more highly specialized ones with spurred nectaries or with closed throats. The flowers of the related families differ little from

those of the snapdragons, as may be seen from the catalpa, ruellia, and trumpet-creeper. This is true also of the bladderworts and the broom-rapes, though the former are submerged water-plants with finely cut leaves and the latter leafless parasites on the roots of honest plants.

The borages pass almost imperceptibly into the verbenas and mints, though the great majority of them can be readily recognized by the regular corolla and five stamens. The highest group, the buglosses, bear irregular flowers and a few of the verbenas and mints have almost perfectly regular corollas. With the exception of a single genus, all of the latter have lost one stamen, and several have lost three, the remaining ones being grouped in pairs. The three families agree in the behavior of the 2-celled ovary, which is subdivided into four cells, each with a single seed. In spite of their close resemblance, the verbenas differ from the mints in the way the style is attached to the ovary, and this suggests that they have arisen from the borages independently. In the latter the style is either terminal or basal, while it is always terminal in the verbenas and basal in the mints. The specialization of the lower lip as a landing platform has been carried to the extreme in the mints and forms the distinctive feature of their flowers. In the highest of these, the sages, monardas and rosemarys, the contrivance for loading pollen on the visitor is probably the most perfect to be found. In the monardas the flowers have become massed in a dense head with special protective leaves and thus suggest the asters or composites. This tendency has been carried further in the globularias, which may be easily mistaken for composites, even the calyx becoming feathery in fruit and adapted to wind transport.

How Pinks Became Plantains and Goosefoots

The simplest of the pink family stand very close indeed to oxalis and flax and may be regarded as more or less direct descendants of them. The characters of their flowers are in close agreement, with the exception of the ovary, which has passed from the 5-celled stage through an intermediate condition of 2-5 imperfect cells to that of a 1-celled ovary in which

the original ancestry is revealed by the separate styles. Although a chickweed looks little like a carnation, they are essentially alike in structure, except for the united sepals of the latter. The most significant change has been the loss of the corolla in several instances, thus foreshadowing the adaptation to wind-pollination so characteristic of the evolution of this family. The latter has given rise to at least three major lines of descent, each one of which ends in the wind-pollinated type of flower.

The shortest and simplest line of descent has given rise to the primroses, which are little more than pinks with united petals. In fact, this advance had already been suggested by the union of the sepals in the fringed pinks and their relatives. With the fusion of the petals has gone the usual reduction of the stamens to a single circle. The sea-lavenders and thrifts stand very close to the primroses, but they have improved the ovary by reducing the number of ovules to a single one. The plantains are also related to the primroses, but the persistence of the cross-wall in the ovary suggests that they may have sprung directly from the pinks with this feature still present. The plantains seem to be still in the process of adjustment to wind-pollination, as the corolla, though present, is papery and minute and the filaments are long and hanging. In the most specialized species, the stamens and pistils are found in separate flowers and the ovary has become one-celled and makes but a single seed.

The portulacas and spring-beauties differ from the pinks chiefly in their fugitive flowers and fleshy leaves, though the larger number of stamens and the greater persistence of cells in the ovary suggest that they may have sprung from the ancestral stock at an earlier time. Another short line of development leads from the pinks to the tamarisks, which are graceful shrubs with tiny leaves and catkin-like flower clusters. The structure of the flower is nearly identical with that of the pinks, but the seeds are plumed at one end. These hairy seeds, the slender spikes, 1-celled pod splitting into two or three parts, and the woody habit indicate that the tamarisks are the

probable ancestors of willows and poplars, in which pollination by the wind has produced the usual effects. The calyx and corolla have disappeared entirely and the staminate and pistillate flowers are on different trees, i.e., the flowers are dioecious.

The major line of advance from the pinks leads to the buckwheats, four-o'clocks, amaranths and goosefoots. It is primarily a response to wind-pollination, though the common buckwheat, hearts-ease and most of the four-o'clocks are pollinated by insects. The beginning of it is best seen in the paronychias, which are so much like the smaller pinks that they have often been placed in the same family. The change to wind-pollination is nicely recorded in the dwindling of the petal to a tiny scale and the reduction of the ovules to one as a rule. In a few cases the petals disappear entirely and the flower becomes essentially that of an amaranth, such as the cockscomb for example. The amaranths and goosefoots are usually regarded as different families, but they are really one, differing only in the degree to which the styles are united and in the texture of the calyx. The most specialized of the goosefoots are the saltbushes, such as the wing-scale and lenscale, in which the plants are woody, the stamens and pistils in separate flowers, and the latter of two forms, the pistillate being enclosed in two large bracts.

The larger number of stamens in buckwheats and four-o'clocks suggests that these may have come from pokeweeds or portulacas rather than from the paronychias. This suggestion receives some support from the fact that they are insect-pollinated for the most part. The four-o'clocks have undergone such a striking special evolution that it is difficult to connect them directly with any of the other families. As in these, the absence of the corolla indicates that they were earlier wind-pollinated, while the brilliant hues of the calyx indicates that they are today pollinated by insects and observation shows that sphinx moths and humming-birds are the regular visitors. Such flowers as those of the bougainvillea have gone a step further in increasing their attraction by converting the involucre around the flowers into a bright corolla-like structure.

Roses and Their Experiments

The rose order is itself marked by three centers in which specialization has been very active. These form the three most important families, which are the roses, peas, and saxifrages. As lineal descendants of the buttercups, the roses come first and are hence regarded as the simplest and lowest. From them the peas and saxifrages have sprung more or less directly, the peas as a unique offshoot and the saxifrages in the line of advancing development. Among the roses the cinq-foils stand nearest the buttercups and are separated from them by the single important difference that the petals are attached to the calyx instead of the receptacle. Among themselves the cinq-foils have carried out most of their experiments on the pistil. This is at first a simple seed-like affair, or achene, with a short smooth style, but the latter may then become long and plumed or jointed. In some cases the achenes remain dry and the receptacle becomes fleshy as in the strawberry; in others the achene itself develops a pulp, such as that of the raspberry, or the receptacle also turns pulpy, as in the blackberry. The causes of this change are not altogether clear, but the advantage gained in securing distribution by animals and man is evident. A similar tendency to develop a pulp is found in the rose-hip, which is a hollow receptacle containing the dry achenes.

The spiræas have advanced to the point of reducing the pistils to five, more or less sunken in the cup-shaped receptacle, which bears the sepals on its margin and the petals and stamens on these, just as in the rose. The red-haw, apple, and pear have arisen from spiræas by the receptacle becoming fleshy and uniting with the papery pistils or carpels, which form the "core" of the apple. In developing into the peach, cherry, plum, and almond, the carpels have decreased to one and the wall of the latter has become fleshy in the outer half for distribution by animals and stony on the inside, thus making a "pit" that protects the seed. As a rule but one of the two seeds develops, though a "philopena" is an almond in which both seeds have matured. The agrimonies have retained the dry fruit of the spiræas, but the carpel is usually solitary and 1-seeded.

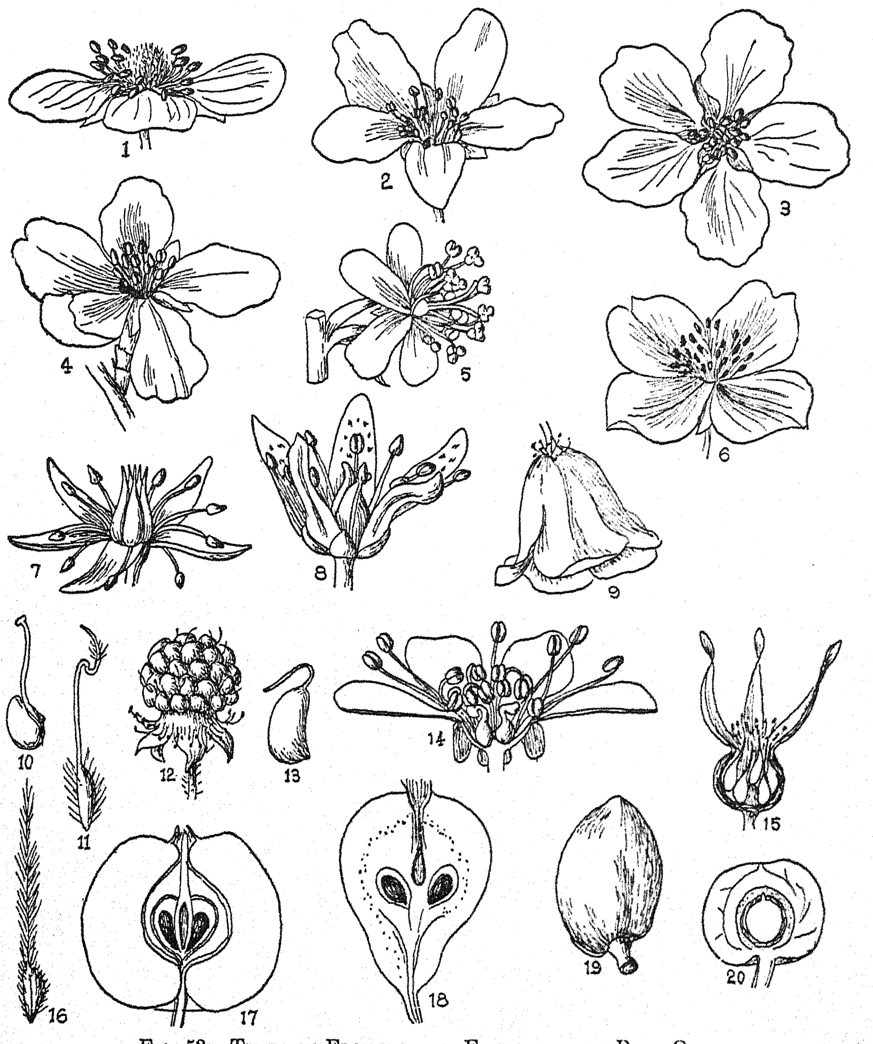

FIG. 53. TYPES OF FLOWERS AND FRUITS IN THE ROSE ORDER
(1) Potentilla; (2) Spiræa; (3) Apple-blossom; (4) Almond-blossom; (5) Agrimony; (6) Mock-orange; (7) Stonecrop; (8) Saxifrage; (9) Gooseberry; (10) Achene of Potentilla; (11) Achene of Geum; (12) Raspberry Fruit; (13) Raspberry Drupelet; (14) Long-section of Spiræa Flower; (15) Long-section of Rose-hip; (16) Achene of Dryas; (17) Section of Apple; (18) Section of Pear; (19) Almond Fruit; (20) Section of Cherry

The peas exhibit the same effect in that the carpels are almost universally solitary, but the receptacle is flat, very much as in the cinq-foils, from which they have apparently sprung. In the mimosas, to which the sensitive plants belong, the corolla is still regular and the stamens many, but in the cassias the latter have decreased to ten and the corolla shows all stages of speciali-

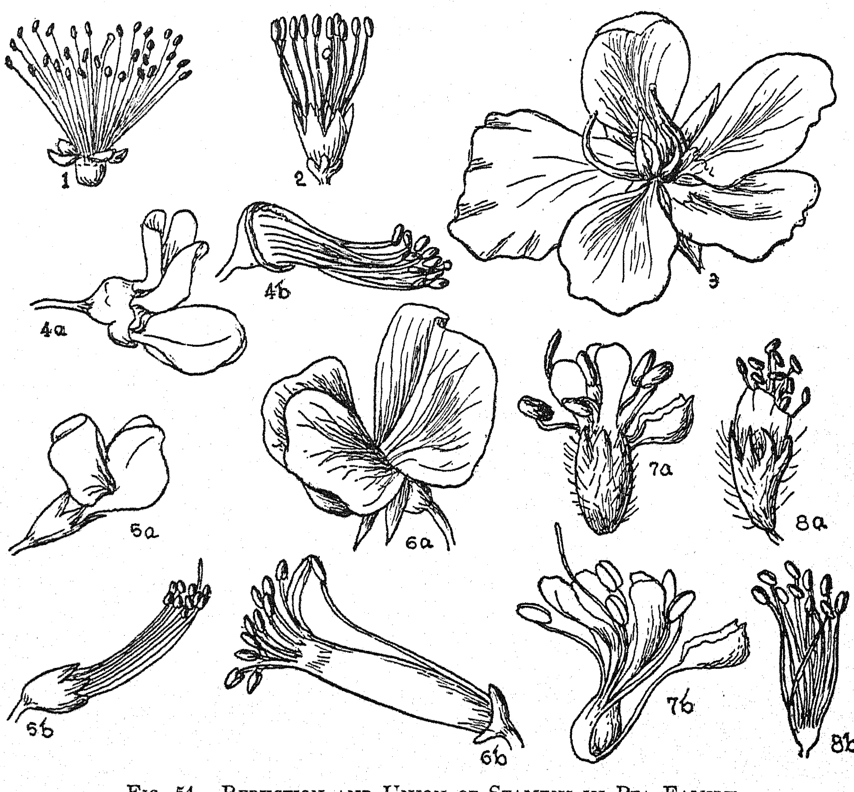

FIG. 54. REDUCTION AND UNION OF STAMENS IN PEA FAMILY
(1) Acacia; (2) Morongia; (3) Cassia; (4) Red-bud; (5) Golden Banner; (6) Sweet-pea; (7) Prairie-clover; (8) Amorpha

zation from regular or nearly so, as in the partridge pea, to irregular or papilionaceous, as in the red-bud. The irregular corolla, consisting of a standard, two wings and a keel, is the rule throughout the peas proper, though this feature is completely lacking in the prairie-clovers and amorphas, which are

such a characteristic feature of the prairies of the Middle West. The behavior of the ten stamens is especially interesting. In the great majority of the true peas, the stamens are in two groups of 9 united and one single, while in the cassias they are all separate. This is likewise true of the lowest peas, such as the false indigos of the prairies; the next step was to combine them into one group, then into two groups of five each, and finally came the typical diadelphous condition. The peas are often termed legumes, from the characteristic 1-celled pod, such as is seen in the bean and the locust, but even this has responded to the universal impulse to limit the number of seeds and sometimes becomes a one-seeded achene but little different from the ancestral form in the cinq-foils.

The saxifrages appear to be connected with the spiræas by two lines of descent. One of these leads to the stonecrops, true saxifrages, escallonias, currants and gooseberries, the other to the mock-oranges and hydrangeas. The first ends blindly in the currants, while the second affords the most probable point of origin for the three lines that spring from the rose order to terminate respectively in cacti, ragweeds, and walnuts.

Rose-Cactus Line of Descent

The mock-oranges are probably direct descendants of the spiræas, differing from the latter chiefly in the union of the carpels into a compound pistil. The result is to produce an inferior ovary and the association of the latter with numerous stamens furnishes the distinguishing mark for the line of descent that terminates in the cacti. There is practically no break in this line as it leaves the rose order, the mock-orange and the common myrtle approaching each other so closely as to seem first cousins. The myrtle family is a large one, comprising the eucalyptus, clove, allspice, guava, etc., and serving as the parent stock of evening primroses on the one hand and cacti on the other. The former have reduced the stamens to a definite number and emphasized the number plan of 4 to the point where it characterizes practically the entire family. In the other direction, the stamens remain numerous and the number of carpels

large as a rule through the meadow-beauties and the ice-plants, and these pass readily into the evening-stars and cacti, in which the partitions of the ovary have disappeared. The ice-plants or mesembryanthemums and the cacti are alike in being fleshy plants, but it is the leaves that are chiefly fleshy in the former and the leafless joints of the stem in the latter, though a few cacti still possess leaves. In the popular mind, nearly all spiny plants are confused under the name "cactus," but this belongs properly only to those plants with the peculiar flower of this family. The ice-plant and the cactus are again alike in having a large number of petals and stamens, a feature that may be associated with the storage of water in the fleshy parts and the consequent ability to render their water supply more secure.

Rose-Sunflower Line of Descent

The hydrangeas differ from the mock-oranges in no important respect, though the ovary usually contains fewer cells, and they might well be combined in the same family. It is likewise but a short step to the witch-hazels in which the ovules are regularly reduced to a single one in each cell. In its turn this family passes almost imperceptibly into the dogwoods, with a single row of stamens instead of two, and these are probably the direct ancestors of the parsleys or umbellifers with their characteristic umbrella-like clusters of flowers. A much more important change was the fusion of the petals by which the dogwoods gave rise to the honeysuckles, probably through the elderberry, which is little more than a dogwood with united petals. Most of the true honeysuckles have made a further advance by grouping the petals into two lips to form an irregular corolla. However, the main line of descent appears to pass through the closely related madders, which have regular corollas, and these are to be regarded as the ancestors of teasels, asters, and bluebells.

The typical flower of the madder family is built on the number plan of 4 or 5, has united petals and an inferior 2-celled ovary with many ovules. Two divergent tendencies have wrought

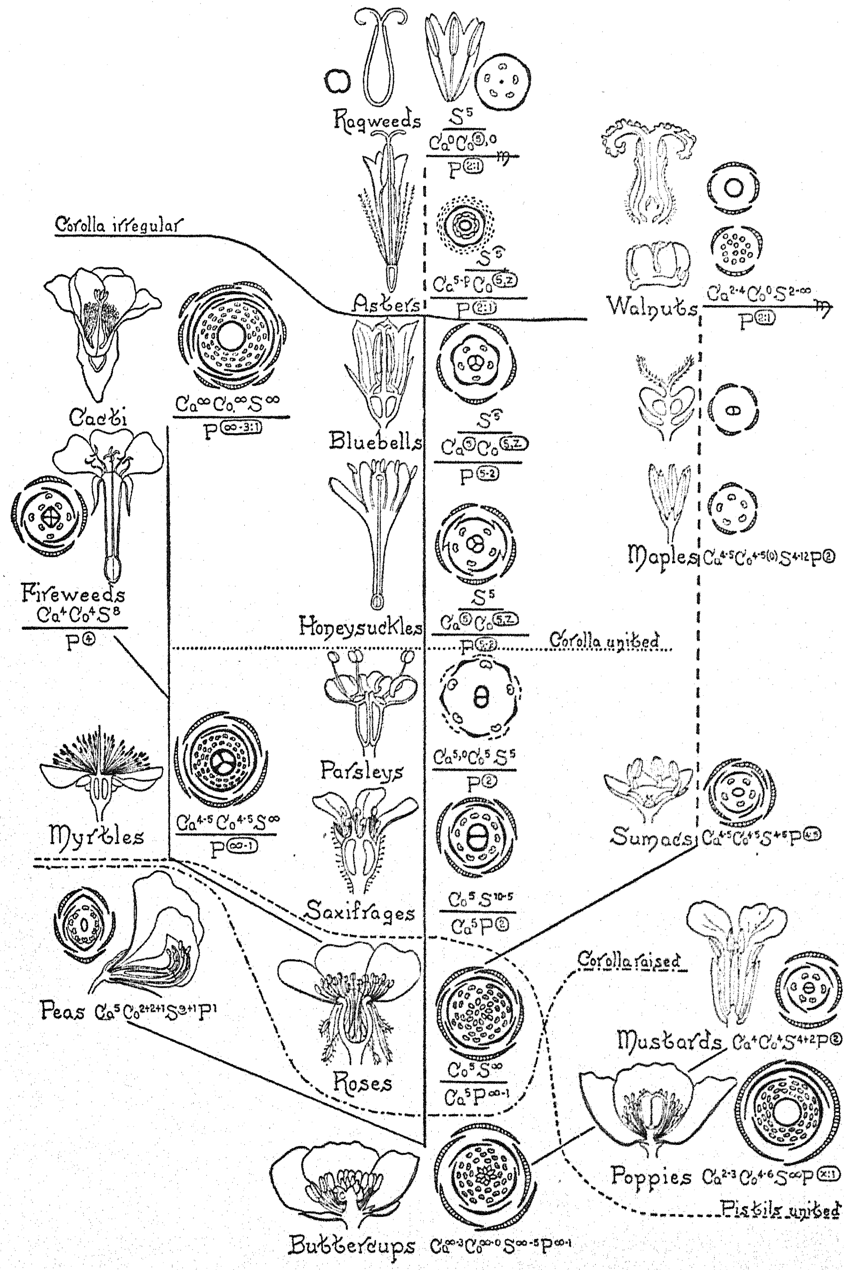

FIG. 55. INSECT AND WIND POLLINATED LINES OF DESCENT FROM ROSES

upon this type, to yield the very different valerians and teasels on the one hand and the bluebells and lobelias on the other. The former are marked by the reduction of the ovary to a single cell containing a solitary ovule, while the latter have left the ovary unchanged, but have become specialized in their pollination by fusing the anthers into a tube and providing the style with hairs for collecting the pollen. These four structures are all characteristic of the great group of asters or composites, but the teasels resemble them especially in the peculiar head of flowers with its involucre, scales, and pappus. However, the asters seem to have come from neither teasels nor bluebells, but to have descended directly from a line that combines the ovary structure of the one with the modification of the anthers and style found in the other. These are the goodenias and brunonias, which are often combined in the same family; some of the former connect directly with the madders, while brunonia exhibits practically every feature found in the composites. The flowers are in a head with involucre and scales, the calyx has become pappus-like, the anthers are united, the style hairy, and the 1-celled, 1-seeded ovary has become a nut-like fruit adapted to wind distribution. The composite flower which approaches this most nearly is the sunflower and its relatives, from which the various tribes of this family are assumed to have sprung. The composite head is really a community of flowers, and is considered later with the grasses as an example of a new type of co-operative evolution.

Rose-Walnut Line of Descent

The witch-hazels and their immediate relatives seem likewise to have been the starting point for the development of bittersweets, sumacs, maples, oaks and walnuts. The first two families stand on nearly the same level, the sumacs being lower in regard to the stamens, which are usually in two rows, and higher in the reduction of the ovule to one. The flowers of buckthorns and vines differ little from these, except in having the stamens opposite the petals instead of alternate and in the valvate rather than imbricate arrangement of the petals in the bud. The general

type of flower in the soapberry family, which comprises horse-chestnuts, maples and bladder-nuts, is essentially that of the ancestral sumacs and bittersweets, but there is a marked tendency to lose the petals and to suppress the stamens in one flower and the pistils in another.

Both of these tendencies become fixed in the birch family, as does also the recurring one toward an inferior ovary. In addition, the staminate flowers have become grouped in long pendulous spikes or catkins, which form a characteristic adaptation to pollination by the wind and hence persist to the end of this line. The gap between the birches, alders and hazel-nuts on the one hand and oaks, beeches and chestnuts on the other is so slight that they have often been included in the same family. This is perhaps the best expression of their relationship, since the oaks and chestnuts are lower as to the ovary, but more specialized with respect to the characteristic cup-like or burr-like involucre of the nut. At the same time there occurs a marked increase in the number of the stamens as a response to wind-pollination and this continues into the walnuts. The advance that marks the latter, however, is the reduction of the ovary to a single cell, though the ancestral number is still indicated by the two stigmas. Furthermore, the fruit has changed from a nut with a scale or involucre to a drupe with a soft outer shell as in the walnut and butternut, or a dry one that splits open, as in the hickory-nut.

WHY THE BOX-ELDER IS A MAPLE

The successive steps in the specialization that results from wind-pollination are strikingly shown by the maples, all of which are regarded as belonging to the single genus *Acer*. The flowers of the soapberry family to which the maples belong usually contain all four parts, and this is likewise true of the simplest species of maple. Many of the American species still bear petals, but these are lacking in the common sugar maple and soft maple. In the latter especially the pistillate flowers bear sterile stamens or staminodes, and the staminate flowers a reduced pistil. It is significant that both these reduced parts

can be made to develop in the usual manner by cutting out the pistil in the one case and the stamens in the other. The greatest specialization in the maple genus occurs in the box-elder, in which petals are completely lost, the sepals often much reduced, and the two kinds of flowers found on different trees. Evidence that the box-elder or its ancestors once had perfect flowers has been afforded by an injured tree, one limb of which bore flowers with both stamens and pistils.

Both the ash and the olive, which belong to the same family (page 99), have undergone a specialization very like that of the maple and one which is also probably taking place at the present time. All the other genera of the olive family have perfect petal-bearing flowers and this is true likewise for the simplest ashes and olives. These have gradually lost their petals, then their sepals, and have not only separated the stamens and pistils, but in the highest species bear them on different trees.

How Arrowheads Became Jack-in-the-Pulpits and Cat-tails

In addition to the main line of evolution leading to the lilies, the arrowheads have also given rise to a second development of much less importance, but one that has yielded many of the common species of our ponds and streams. The habit of growing in water probably led to a change from insect to wind-pollination and the consequences are soon seen in the gradual disappearance of calyx and corolla and the separation of the stamens and pistils. The first stage is found in the arrow-grasses, in which the calyx and corolla are essentially alike in form and color and the pistils are more or less united. In the closely related pondweeds the adjustment goes further and the corolla is lost, followed by the calyx, and then by the reduction and separation of the stamens and pistils as the plants become more and more submerged. In another direction the first change consists in reducing the partitions of the compound pistil and the specialization of an upper leaf to form a floral bract or spathe. This is the condition found in the sweet-flag, which appears to be the forerunner of both the arums and the cat-tails. The former have made much of the spathe as an organ

of attraction and protection, while the cat-tails have turned their attention to a more complete adaptation to wind-pollination. The odd and often grotesque appearance of the calla, jack-in-the-pulpit, skunk-cabbage and other arums is due to the central column of tiny flowers more or less enfolded in the colored leafy spathe. With the development of the latter has gone the disappearance of the perianth and the separation of the stamens and pistils.

Lilies and Their Experiments

The outstanding feature of the lily order has been the change in the work of the calyx and corolla. In the arrowheads the green calyx performs its usual tasks of protection and nutrition, while the white corolla serves for attraction. This normal relation persists among the lower families of the lily order, such as the spiderworts, and even extends to some members of the lily family itself, like the wake-robins and mariposa lilies. In the vast majority of the family, the calyx is colored like the corolla and the two are not readily distinguishable, thus greatly increasing the attraction of the lily, tulip, hyacinth and other flowers for insects and man. From such flowers have sprung the amaryllis and iris of even greater showiness and beauty. In another direction the small white petals of such flowers as the false Solomons-seal and the mayflower have led to the whitish or greenish ones of the Solomons-seal, asparagus, and smilax as they tended to share the work of the sepals. With the complete change to wind-pollination the entire perianth became green, resulting in the typical flower of the rushes, which differs from that of the lily in no important structural feature, though they look wholly unlike.

Within the vast lily family the structure of the flower remains remarkably constant, only a very few genera of the two or three hundred suggesting the advances that are wrought out in the orchid and grass orders. In one or two the number plan is 2 or 4 instead of 3, or the flower may be more or less irregular, while in a few others the stamens may be reduced to 3 or the 3 cells of the pistil merged into one. These changes give character to

the flowers of the pickerel-weed family, to which the common water-hyacinth belongs. The perianth is irregular, the stamens often three and the ovary 1-celled.

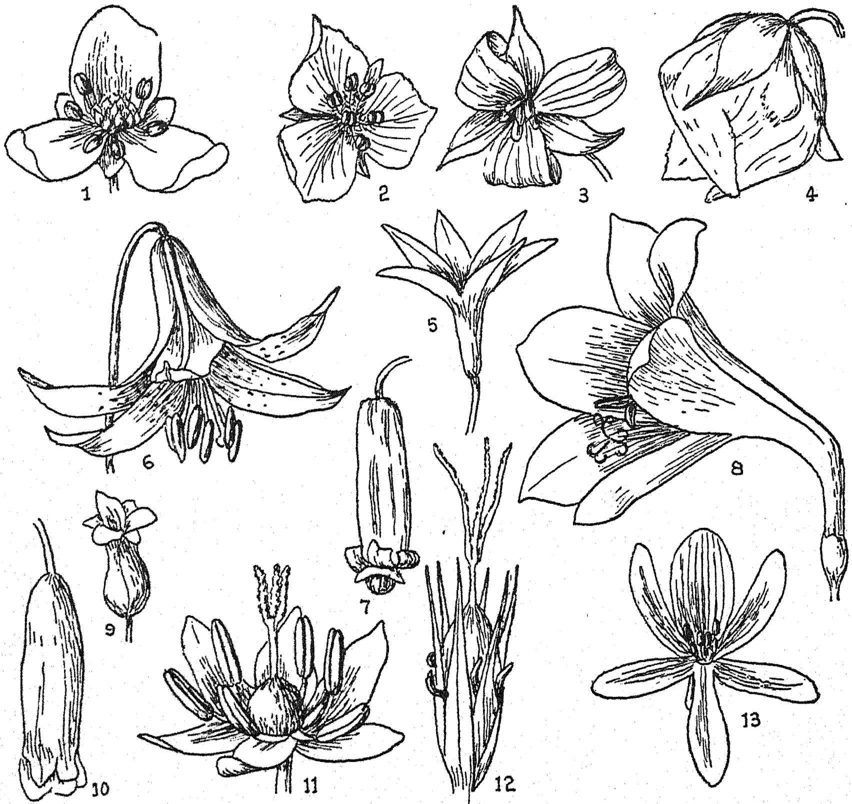

FIG. 56. LILIES AND THEIR EXPERIMENTS
(1) Alisma; (2) Spiderwort; (3) Trillium; (4) Fairy Lantern; (5) Golden-stars; (6) Canada Lily; (7) Firecracker-flower; (8) Watsonia; (9) Asparagus; (10) Solomons-seal; (11) Luzula; (12) Rush; (13) Water-hyacinth

THE ANCESTRY OF THE PALMS

The palms are little more than arborescent lilies. In comparison with the lowly habit of the rushes, the tree-form of the palms appears to have hastened the response to wind-pollination. While the rushes bear perfect flowers as a rule, those of the

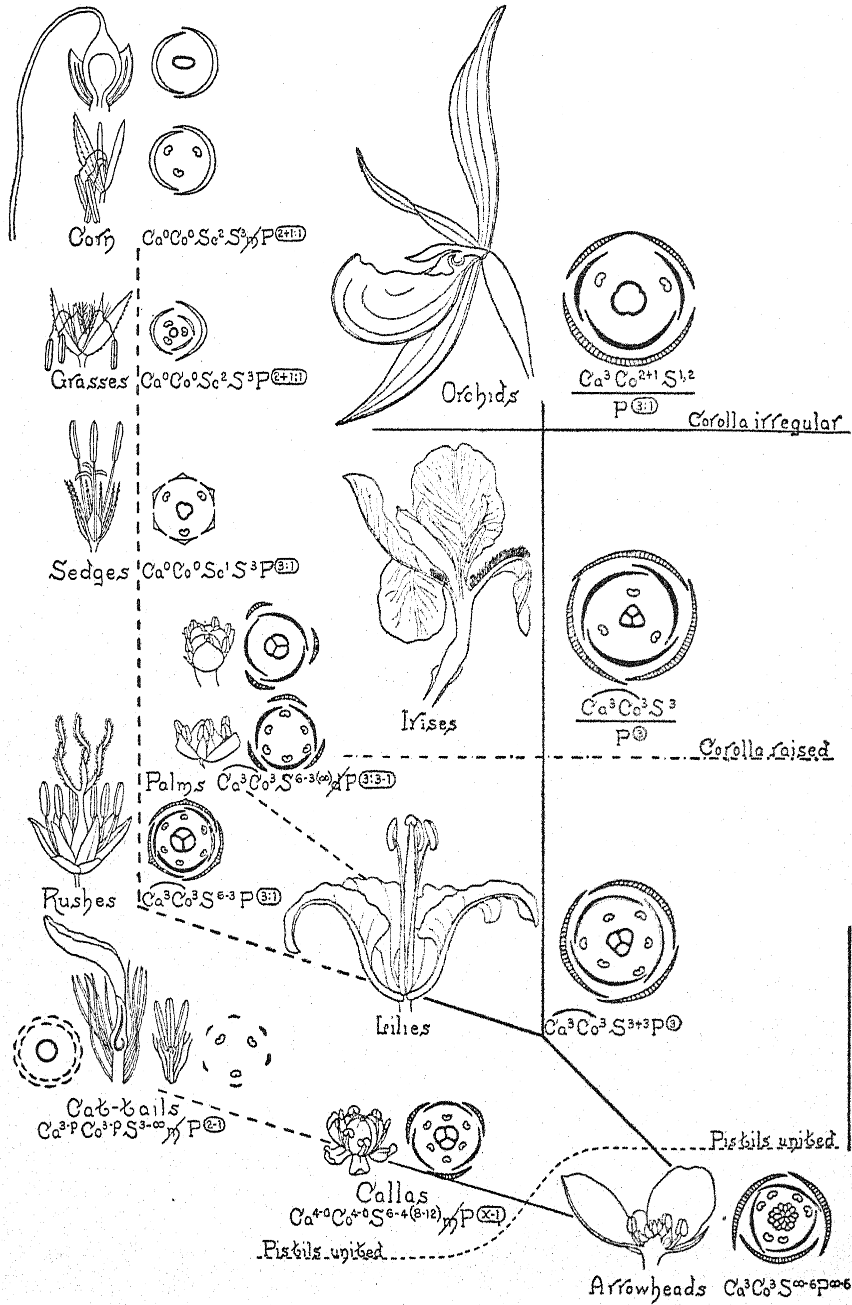

FIG. 57. INSECT AND WIND POLLINATED LINES OF DESCENT FROM LILIES

palms are typically monoecious or dioecious. Perfect flowers occur in but two genera, one of them our palmetto, though some perfect flowers occur now and then in some monoecious genera. The palms seem to be in the midst of active specialization, since petals and sepals, though alike, are still commonly present, being reduced or obsolete in but two genera. The stamens are regularly six as yet, three being found in but a few species. The reduction of the 3-celled ovary often results in a 1-celled fruit which is then 1-seeded, as the ovules are solitary in each cell. Like most wind-pollinated plants, especially trees, palms have enormously increased the number of flowers as the size has diminished, some individuals bearing more than a half-million flowers. The genera are numerous and the species exceed a thousand in number, indicating that another great line of wind-pollination is in process of rapid evolution.

Lily-Orchid Line of Descent

The transition from the lilies to the iris order is one of the most direct, though it has evidently taken place in two directions, and has to do only with the position of the ovary. The elevation of the perianth is merely foreshadowed in a few of the lily family, but the entire process is revealed in the hæmodorum family, which passes from superior to half-inferior and then to completely inferior ovaries. The amaryllis family, including the daffodils, narcissus, snowdrop, tuberose and century plant, is marked by complete elevation of the perianth (epigyny) and appears to have sprung from lilies directly. This is supported by the fact that lilies exhibit both imbricate and valvate estivation, while the amaryllises show only the imbricate type and the hæmodorums only the valvate. The irises, comprising crocus, blue-eyed grass or grass-iris, ixia, gladiolus, etc., have arisen from the amaryllises chiefly by the suppression of one circle of 3 stamens, though they differ also in the minor features of convolute estivation and extrorse anthers. They appear to represent the culmination of the development of the essentially regular showy flower so characteristic of the lily, amaryllis and iris families.

All the other lines of development seem to have sprung from the hæmodorum rather than the amaryllis family, as indicated by the valvate estivation. The yams have diverged chiefly as a consequence of separating the stamens and pistils, though they are also unique in their climbing stems. The bromelias, which include the pineapple and Spanish moss, differ from the hæmodorums in no essential character, apart from the fact that the outer segments of the perianth have resumed the characters of a calyx. This seeming reversion persists through the canna family, which includes likewise the ginger, arrowroot and banana. In these the number of stamens has been reduced as a rule to one and the ovules from many to few. The gingers and arrowroots terminate this line of development and it is necessary to turn again to the hæmodorums for the changes that produced the orchids.

It is probable that the first step toward the orchids was taken by members of the frogs-bit family with complete flowers, but these are now practically all diclinic and aquatic. Apart from this they agree essentially with the burmannias in flower structure and especially in regard to the ovary, ovules and seed. They are the first family in this line to produce numerous small seeds without albumen, a type carried to the extreme in the next two families. The burmannias approach the orchids in the reduction of the stamens to 3, the innumerable tiny seeds and the lip-like development of one of the segments of the perianth. The next step in the reduction of the stamens in consequence of improved pollination is shown by the lady-slipper with two, while all other orchids possess but a single one, usually with the rudiments of two others. The remarkable irregularity of the perianth, the union of the style and the stamens, the formation of pollinia and the myriad of microscopic seeds set the orchids apart as the most highly specialized of insect-pollinated monocotyledons. They stand in unique contrast to the other great terminal groups, composites, mints, goosefoots, walnuts and grasses, in which the production of a one-seeded fruit appears as the chief outcome of specialization.

Lily-Grass Line of Descent

We have already seen that there is no important difference in the flower structure of the insect-pollinated lilies and the wind-pollinated rushes. However, to the casual observer they seem as far apart as the poles in attractiveness, many of the true lilies being several inches across and of the most brilliant hues, while the rush flower is a quarter of an inch wide or less and a dull brown or green in tone. In addition, the flowers are numerous and they are dry or rigid in texture in contrast to the delicate fleshy or waxy ones of the lily. The anthers are borne on lengthened filaments, more easily shaken in the wind, and the stigmas have become long and slender to offer more surface for catching pollen. It is significant that the tepals or parts of the perianth remain essentially alike in size and color, in spite of the profound change from insect to wind-pollination. This serves to explain the disappearance of both calyx and corolla in the sedges and grasses and the development of glumes to replace them in some measure. It may also be significant that the rushes, restions and sedges are almost universally swamp plants, since swamps must have formerly constituted the chief open spaces in which herbs might develop wind-pollinated flowers.

The restions or rope-sedges stand between the rushes and the true sedges, though it seems probable that the main line of descent did not pass directly through them. The most important advances are four in number, namely, decrease of the stamens from 6 to 3, reduction of the ovary to one cell and the ovules to one, and the separation of the stamens and pistils in different flowers. All of the changes can be found in the rushes, but they are exceptional there and become the rule only in the rope-sedges. In a few of the latter the inner tepals disappear and thus foreshadow the loss of the perianth in the sedges. In one genus of these the tepals still persist as distinct scales, while in others they are represented by bristles. With the disappearance of the perianth has come the emphasis of the bract that covers it, a feature already present in the restions, but developed in

the sedges to the point where it becomes the characteristic feature of the flower cluster or spikelet. In some sedges the lowermost flowers of the spikelet fail to develop and in consequence several empty bracts or glumes appear at the base. When this happens in sedges with the flowers in two rows, as in the galingale, a close approach is made to the simpler grasses, such as the bamboos. These have the pistil and stamens, perianth relics and 3-4 empty glumes of sedges; the striking departure consists in enclosing each flower in two scales or glumes, which are typical of grasses. In the vast majority of the latter, moreover, the pistil is further modified to become the most efficient known, two of the carpels being transformed into bushy styles and the other into an ovary merely. Meanwhile, the stamens have been increasingly specialized in the restions and sedges, until in the grasses they have become perfectly adapted to pollen transport by the wind.

Like the composite head, the grass spikelet has undergone further evolution and reduction. Both are to be regarded as flower "communities" and represent the highest stage of advancement reached under insect- and wind-pollination respectively.

Community or Social Flowers

The working of the law of conservation is seen in the fact that most plants bear flowers in clusters rather than singly. Although solitary flowers can be given more parental care, in some respects this places too low a limit on the number of effective seeds. Grouping flowers in clusters or inflorescences tends to increase the mass of attractive color and also enables insect visitors to work more rapidly and efficiently. As a result of these three decisive advantages, even the lower flowers have experimented with various groupings and the tendency to co-operation increases regularly with specialization. It occurs in both insect and wind flowers, though the advantages arising from it are most marked in the former. It is easy to understand why it has proved most effective or necessary with small flowers, and consequently why such co-operative flower groups are most numerous and most successful in the rose-aster line

of descent from clovers onward. Lilies, geraniums, and their descendants produce relatively large flowers as a rule and the clusters usually contain few flowers or these are not closely aggregated, the most striking exceptions being hyacinths, phloxes, hearts-ease, etc. Among the flowers of the rose order, the grouping is often close as in spiræa, hawthorn, choke-cherry, hydrangea and most of the pea family, or is so compact as to result in a

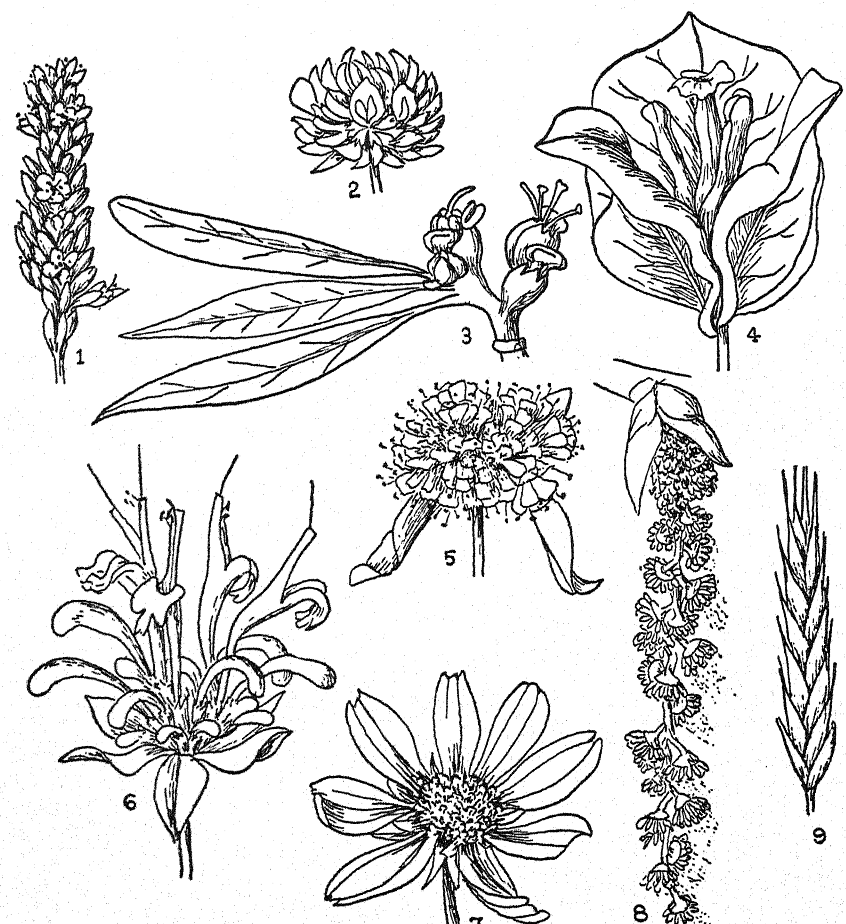

FIG. 58. COMMUNITY FLOWERS
(1) Knotweed; (2) White Clover; (3) Poinsettia; (4) Bougainvillea; (5) Golden Buckwheat; (6) Horse-mint; (7) Dwarf Sunflower; (8) Cottonwood; (9) Brome-grass

head or spike, such as that of the clover, prairie-clover and purple amorpha.

The advantages of crowding small flowers in a dense head are well shown by the red clover with its mass of brilliant color and its gain in protection and economy of material. Some of its relatives go a step further and fashion an involucre out of floral leaves, thus increasing the protection and food-supply of the cluster. In certain species these leaves or bracts are separate, and in others they are united to furnish still further protection. A similar solution has been found by flowers of widely different form and ancestry, usually with the consequence that the cluster or community is mistaken for a single flower. A familiar example of this is the flowering dogwood, which owes its name to the four white bracts that imitate petals. The real flowers of the poinsettia are tiny affairs crowded in an involucre, the ornamental feature of the plant being the encircling leaves with their scarlet bases. In the four-o'clocks the involucre is often mistaken for a calyx until it is seen to contain several flowers, and the beauty of the related bougainvillea comes from the purple of the corolla-like bracts. More surprising still is to find that the flower of the jack-in-the-pulpit and the calla "lily" is a colored bract, the real flowers being easily overlooked on the crowded central column.

The tendency to make dense clusters increases toward the upper end of the six lines of descent, with the exception of the lily-orchid line with its large handsome flowers. It is marked in the mints and verbenas, the cluster appearing as a dense head with an involucre in the horse-mint, many of the salvias and especially in the globularias. The "flower" of eriogonum, a relative of the buckwheat and hearts-ease, is actually a tiny head, which is sometimes densely aggregated to form a large and compound head. The catkins of birches, oaks and walnuts are co-operative communities to a considerable extent, and the spikelets of sedges and grasses are much better examples of this advance. But the most successful application of the principle of co-operation is found in the aster, daisy, sunflower and dandelion, largely as a result of the experience acquired by the

small flowers of their ancestors. The head or cluster of flowers characteristic of the aster family is the outstanding example of co-operation among flowers, and serves to explain why the term "composite" is often applied to it.

Origin and Work of the Sunflower Head

The experiences that led to the high degree of co-operation found in the sunflower head probably operated upon such a

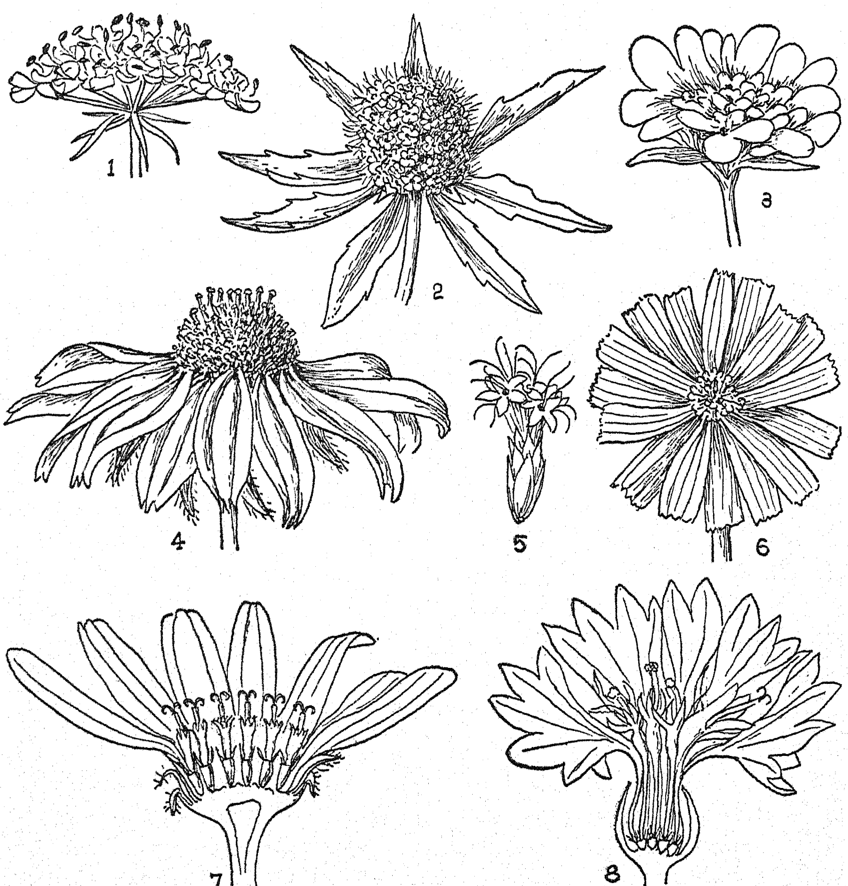

Fig. 59. Types of Compound Clusters
(1) Heracle; (2) Sea-holly; (3) Scabiosa; (4) Black-eyed Susan; (5) Blazing-star; (6) Chicory; (7) Section of Sunflower; (8) Section of Bachelors-button

flower cluster as that of the caraway, carrot and fennel. All of these belong to the parsley family, which are often called umbellifers because the small flowers are borne in umbels or umbrella-like clusters. The flowers are closely grouped on the same level and the attractive effect of each individual is greatly enhanced. In some instances, they are densely crowded and already possess a distinct involucre, as may be seen in the blue lace-flower and the sea-holly of the gardens. The individual flower stalks arise from the same point and are about equal in length. At the base of each is often to be found a small bract, similar to the more conspicuous ones of open inflorescences. The advantages to be gained by saving material and energy and by bringing the flowers closer together to form a more solid mass of color have gradually led to the shortening and then to the disappearance of the individual stalks, thus turning the umbel into a head. This was usually accompanied by a shortening of the axis, which brought the upper leaves or bracts into rows to form an involucre. Within the head the bracts of the umbel or spike sometimes persisted as a scale about each floret in the sunflower and its relatives, though these scales or chaff have usually disappeared in the other groups of composites. They now have little or no work to do and have become papery and colorless as a rule. In contrast, the scales of the involucre are nearly always green and often large and leaf-like, so that they serve both to protect and nourish the community of flowers within.

The dense crowding of the florets in a head has a number of interesting consequences. The first of these is to make unnecessary the protective work of the calyx and to render impossible its regular task of food-making. The green color and leaf-like texture are lost and the free tips of the sepals become papery scales or slender bristles, often of value in scattering the seed-like fruits. More important has been the readjustment of the tasks of pollination in such a compact community. Each floret is so small that the opening of the anthers fills it full of pollen that must be swept out if self-pollination is to be avoided. This is accomplished by brushes on the style, the two lobes of

the latter being tightly pressed together until they project fully from the corolla tube, when they separate widely and expose the receptive surface to cross-pollination by means of insects. Later, the stigmatic lobes turn and twist, bringing their surfaces in contact with the pollen masses on the brushes and thus making self-pollination possible in those cases where crossing has failed for any reason. Crowding also restricts the further development of the central flowers and hence contributes indirectly to the change of the outer row into ribbon-like ray florets. It likewise places a premium upon new methods of distributing the seeds, if the

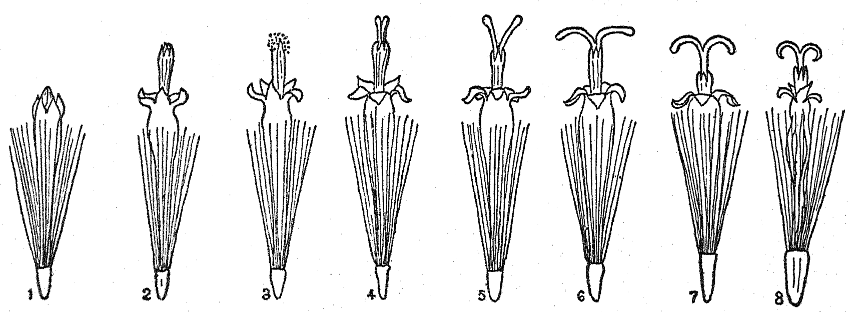

FIG. 60. POLLINATION STORY OF SENECIO FLORET

large number found in most heads are to have a fair chance of germination and survival.

SPECIALIZATION OF THE HEAD

The head is to be regarded as a community of flowers with new needs and new opportunities, in which division of labor and consequent co-operation are the guiding social principles. Its great significance lies in the fact that the group has now assumed the tasks of protection and nutrition, of attraction and dissemination that were formerly discharged by the individual flower. It has accomplished this by dividing up the labor, conserving materials and increasing the community care of flower and offspring. This has been done under the compelling guidance of both insect and wind-pollination, though the latter is recent and concerns a relatively small number of species. The most striking division of labor has resulted from the change of the

outer florets of the head, in which the tubular corolla has been modified into a strap-shaped or ligulate one. This was probably at first the result of freedom from crowding and of the operation of light and gravity, but its value in attraction doubtless led to an increasing emphasis upon it. With this, or sometimes quite apart from it, went a further specialization, as a result of which stamens or pistils, or sometimes both, became useless in the ray-flowers and hence tended to disappear more or less completely.

The head also furnished scope for both individual and community progress in the task of securing the distribution of seed. No other family can compare with the composites in the number,

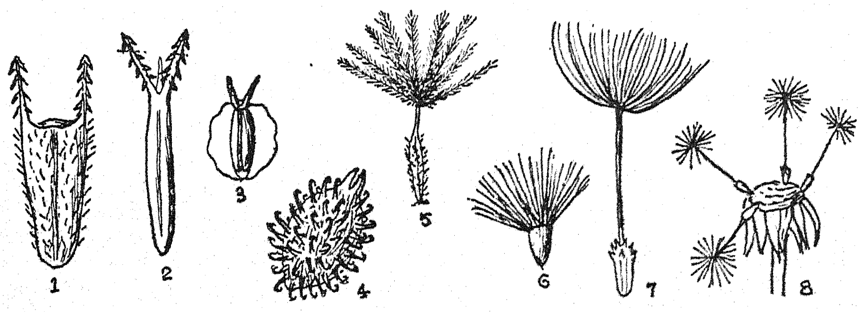

FIG. 61. MODIFICATIONS OF COMPOSITE FRUITS FOR DISTRIBUTION
(1, 2) Tickseeds; (3) Coreopsis; (4) Cocklebur; (5) Salsify; (6) Thistle; (7, 8) Dandelion

variety and perfection of devices for dissemination. Most of these make use of the wind for transport, but some of them are carried by attachment, as in the case of cosmos, coreopsis and the various tickseeds. The carriage of the individual fruit reaches its greatest perfection in the asters, thistles and above all the dandelions, which are provided with a parachute that unfolds for flight. When the community assumes the task of distribution, it makes use of attachment, a familiar example being the hooked prickles of the burdock head. A similar method is employed by the cockle-bur, which further increases the chances of successful home-making by reducing the seeds to two and insuring that these germinate at different times. The com-

munity is also concerned with providing a proper "take-off" platform for parachute fruits at the beginning of their flight. This is beautifully illustrated by the stalks of dandelion and its relatives in which the involucre not only flattens and recurves to free the fruits, but the stalk also stretches upward to three or four times its length and places them above other species that act as obstacles. It is just this habit of the dandelion that causes lawns to wear a ragged look.

GENERAL FEATURES OF THE COMPOSITE TRIBES

Although the general features of the floret remain much the same in the various groups of composites, the form undergoes several striking changes. The change of the marginal flowers of the disk into strap-shaped ones probably occurred very early, since it is the rule in both the sunflowers and the sneezeweeds, which are regarded as the ancestors of all other composites. The usual form of head consequently is one with a marginal row of show or ray-florets enclosing a center of small tubular disk-florets devoted to the task of seed-making. The ray-floret is little more than a tubular one that has grown lop-sided to form a flaunting banner, and an illuminating hint of the steps in this process may often be obtained from cornflowers and gaillardias, where the rays show more or less of the original tube form. Under certain conditions the ray-flowers may fail to develop, and this becomes a regular feature of the ironweed and boneset tribes, where the head consists of tubular disk-flowers alone. Cultivation frequently leads to the "doubling" of the head, by which all of the florets become strap-shaped, and a somewhat similar process in nature has produced such heads as those of the dandelion, lettuce and chicory. In both cases it seems a just inference to assume that increased attraction has been a factor, though in one instance this has acted upon man and in the other, pollinating insects. The florets of the thistle head are all alike in being tubular, though they differ much from the usual form of disk-flower, and in a related group, the mutisias, the corolla has become irregular and two-lipped, much like that of mints.

It is now easy to understand why the head of an aster, dahlia or marigold is commonly mistaken for a single flower and why the sunflower has received its name. The community of flowers that form the head have worked together to solve the same problems of attraction, protection and distribution that formerly confronted the individual flower, and the solutions found have been of the same general character. In spite of differences in structure and origin, the green involucre of the sunflower head performs the same tasks as the green calyx of a hollyhock. It protects the young flowers in the bud and provides food for them as well as for the new plants wrapped up in the seeds. The border of pennant-like ray-flowers serves to attract insects and to furnish a landing-platform for them just as the corolla does this for the single flower. The ovary of the latter sometimes takes over the task of distribution, as in the case of the bed-straws, and this is now and then true of the involucre, such as that of the burdock and cockle-bur. The head itself is the result of the advantages to be gained from grouping, and, once the rule for composites, is then employed like the single flower of simpler families to produce greater attraction by means of various kinds of grouping.

The striking adaptation of the composites to insect-pollination probably explains why they have so rarely resorted to pollination by wind. This has occurred typically in the ragweed tribe, which in consequence produces small greenish heads that easily elude the eye. These have sprung from the sunflowers and rosinweeds, in which response to the wind has led to the gradual reduction of the ray-flowers. This change appears to have been a relatively recent one, since the steps in advance form a perfect series from the rosinweeds to the highest of the ragweeds, which is the cockle-bur. The ancestral head is still bright-colored and possesses small rays, while the anthers are characteristically united and straight at the tip. In the simplest ragweed, iva, the color has become greenish, the rays have disappeared, and the anthers are nearly free and the appendages inflexed. The next step is the loss of the corolla of the pistillate flowers, and this is followed by the specialization of the heads so that some contain

only stamens, the others only pistils, though both kinds occur on the same plant. At the same time the number of pistil flowers is reduced so that the head becomes one-flowered. In the simplest form the bracts of the involucre remain separate, but they soon unite to form a calyx-like cup, the condition found in the ragweeds proper. Union then begins to operate on these one-flowered heads to make a compound head, as in franseria, which further develops spines for distribution by animals. In the cockle-bur, the number of simple heads in the compound one is reduced from four to two, and in rare cases to a single one, which is probably to be the final outcome. This is foreshadowed by the fact that the two seeds regularly germinate at different times. The involucre has become completely closed and is provided with hooked barbs to form one of the best of all devices for carriage by attachment.

Origin and Work of the Grass Spikelet

The regular consequence of the transition from insect to wind-pollination is a marked reduction in the size of the flower. Nowhere is this more striking than in the lilies, the flower of the largest tiger-lilies exceeding by a hundred fold that of many of the rushes. The small size of the latter furnishes the usual incentive for the association of the individual flowers into communities, although the advantage of increased attraction is lacking in these wind-pollinated flowers. However, the need of mutual protection is enhanced and this is accompanied in some degree by that of nutrition. This tendency to form a dense cluster or spike prevails throughout the rush family, becomes controlling in the rope-sedges, and furnishes the characteristic feature of sedges and grasses. In the latter, the flower becomes almost microscopical, while the cluster or spikelet itself is much smaller than the vast majority of insect-pollinated flowers.

The spikelet in the sedges follows the rule as to number, the flowers being numerous in the lower genera and the number decreasing more or less regularly as specialization advances. In one direction the radiate spike becomes two-sided, the florets occurring in rows on either side of the axis. The florets are

almost wholly concealed by the bracts or glumes, which give a parchment-like texture to the spikelet. Even in the sedges there is a tendency for the lower flowers to dwindle and some of the basal bracts become empty in consequence, serving for protection to a certain degree. This process is emphasized in the grasses, where it results all but universally in two empty glumes at the base of each spikelet. The nutritive and protective functions of the glumes are usually increased at the same time, espe-

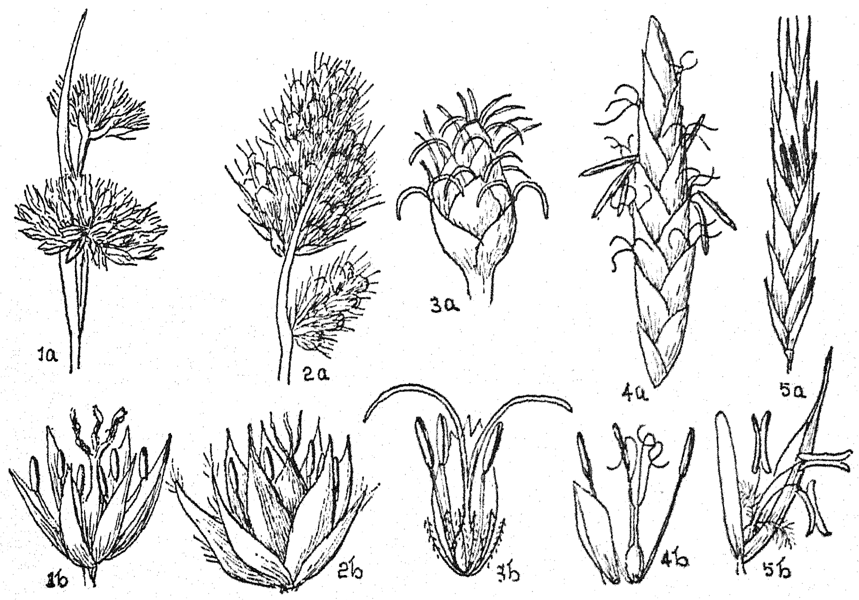

Fig. 62. Fore-runners of Grasses
(a, cluster or spikelet; b, flower)
Rushes (1) Juncus; (2) Luzula; Sedges (3) Scirpus; (4) Cyperus; Grass (5) Brome-grass

cially in such grasses as the oat, where the glumes enclose the entire spikelet. In addition, two similar papery bracts or lemmas develop to enclose each floret, providing it with further protection and nutrition. However, the protecting lemmas are stiff and do not readily open to permit pollination. This need is met by scales or pads of tissue that may represent the tepals of rushes and lilies. In the presence of glume and lemma, these

are now as useless for protection and nutrition as for attraction, but are available for a new task. This is found in the need of forcing the lemmas apart for the exsertion of stamens and stigmas, and the useless tepals, now called lodicules, accomplish this by their ability to swell.

COMPARISON OF SPIKELET AND HEAD

The spikelet of a grass looks so unlike the head of a sunflower or dandelion as to warrant the feeling that they have nothing whatever in common. Yet they are merely two expressions of the same fundamental process, the striking differences between them arising from the fact that grasses are pollinated by the wind, composites by insects. The intrinsic resemblance lies in the presence of a flower community, the specialization of floral leaves or bracts for particular purposes, the transformation of useless parts into structures with new functions, and most striking of all, the production of a new feature, the spikelet or the head, on which the processes of evolution will operate in essentially the same manner as on the individual flower. In both origin and structure, the empty glumes of the grass spikelet are the counterparts of the bracts that surround the sunflower head, while the lemmas correspond to the chaff or scales between the disk-florets of the sunflower. In the composites, the calyx, now useless because the task of protecting and feeding the florets is assumed by the bracts, is converted into a colorless pappus utilized for dissemination; the grass calyx or perianth undergoes similar reduction, but it is modified into a device for opening the flower. The explanation of this difference in fate is perhaps to be sought in the fact that the calyx encloses the ovary in composites, but is below and free from it in the grasses.

As previously suggested, the almost total lack of resemblance between spikelet and head is due to the fact that the latter has emphasized attraction as a feature of insect-pollination. The circle of ray-florets in the sunflower is not only a consequence of this, but is at the same time the most conspicuous part of the head, by contrast supporting the popular belief that grasses possess no flowers. The essential similarity of the two is exem-

plified by the wind-pollinated composites, such as ragweeds and cockle-burs, and is repeatedly disclosed in the further specialization of both spikelet and head. Not only is there a steady reduction in the number of florets and an increasing tendency toward one-flowered clusters, but these in turn exhibit a trend toward aggregation into compound clusters, with renewed possibilities of specialization. The most striking example of this is an ear of corn, in which the spikelets are represented by the kernels, the chaff being the disappearing glumes and lemmas. The cob, apparently a new structure, is really the fused and enlarged axis, while the husks are obviously the leaves of a new kind of involucre.

BAMBOOS AND BLUEGRASSES

The grasses further resemble the composites in the development of more than a dozen tribes exhibiting a diversity of evolution that is evidently the direct outcome of the new social structure, the spikelet and the head. In seeking to determine the relative position of the various tribes, the same principles apply as in the case of the composites and flowering plants generally. The floret is now the unit of the spikelet and hence those grasses with the largest number of flowers in the latter are to be considered the simplest or lowest. By this test the bamboos take the initial position, a conclusion strikingly supported by the regular presence of 3 lodicules as relics of the former perianth of rushes, of 3, 4, or even 10 glumes, and frequently of 3 styles and 6 stamens. The bluegrasses are most closely related to the bamboos, as the many-flowered spikelet indicates, but the lodicules are reduced to 2 small scales, the stamens are regularly 3 and the styles 2, advances that are to characterize all the higher tribes. Like the buttercups but to a lesser degree, they have experimented with other changes which are to be successfully carried out by higher tribes, such as the reduction of the spikelet to a single flower.

EVOLUTION AND RELATIONSHIP OF GRASS TRIBES

It appears probable that the spikelet of the bluegrasses early exhibited differences in the nutritive correlation of the flowers,

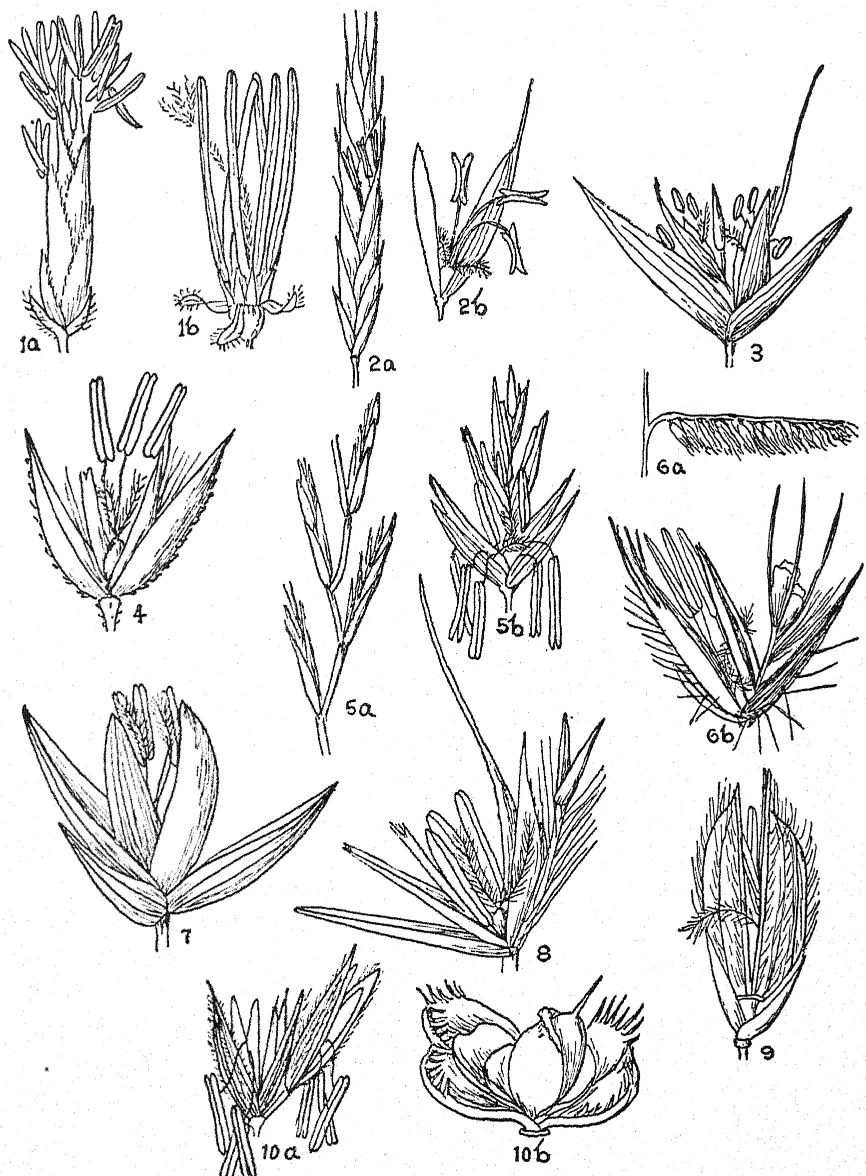

FIG. 63. FLOWER CLUSTERS AND FLOWERS OF IMPORTANT TRIBES OF GRASSES
(1) Bamboo; (2) Brome-grass; (3) Oats; (4) Bluejoint-grass; (5) Wheat-grass; (6) Grama-grass; (7) Panic-grass; (8) Red-stem; (9) Rice; (10) Corn, staminate and pistillate flowers

resulting to the advantage of the basal floret in some and the apical one in others. Thus, in the former case the insufficiently nourished and hence sterile or reduced florets are at the tip of the spikelet, and in the latter they are at the base. With these are correlated other features; the spikelet of the basal type is jointed above the glumes, the axis possesses internodes between the florets and is often continued above them. In the apical type the joint is below the glumes, the entire spikelet falling as a unit, and there are no internodes or projecting rachilla. Occasional exceptions to the rule do occur and consequently serve to indicate the common origin of the groups concerned. On this basis the grasses fall into two subfamilies that apparently diverged from the immediate ancestors of the present bluegrasses. Specialization and consequent reduction obviously operated much more rapidly upon the apical type, since these rarely contain more than a single fertile floret. On the other hand, four of the six tribes belonging to the basal type possess spikelets with two or more flowers, and the course of evolution is correspondingly clearer. It is of interest, and possibly of significance, in this connection that these genera are typically temperate or boreal in distribution, while those of the apical type are predominantly tropical or subtropical and relatively recent.

The bluegrasses proper have evolved in two major directions, one marked by the reduction of the spikelet to a single flower, the other by the crowding of the spikelets into a dense two-rowed spike. Cylindric spikes are occasional in the first case, and the tendency toward single-flowered spikelets occurs frequently in the second. There is no clear-cut line of division between the bluegrass and the oat tribes, the difference being chiefly one of emphasis. In the latter, the glumes usually enclose the spikelet largely or wholly, there is a regular tendency to form 2-flowered spikelets, and the lemma is typically awned on the back rather than at the tip. A few genera possess 1-flowered spikelets and these suggest the transition to the terminal tribe of red-tops or bent-grasses. These occasionally betray their ancestry by vestiges of a second floret, or in one species by a complete flower. As a whole, this tribe is probably to be re-

garded as the most advanced of all, but single genera of other tribes, such as the corn and buffalo-grass, show still greater specialization in a number of respects.

The barleys and chlorids are supposed to represent the two branches of a common line of descent from bluegrasses, since both are characterized by the arrangement of the spikelets in a two-rowed spike. The distinction between the two tribes lies in the nature of the spike, which is equilateral in barleys and one-sided in the chlorids. The axis or rachis in the former is typically zig-zag or jointed. About half the genera of each have developed 1-flowered spikelets, but the highest stage of specialization is attained by the chlorids, in which the buffalo-grasses bear the stamens and pistils in different clusters, the staminate finally becoming 1-flowered.

The phalarids are intermediate between the bluegrass and the panic-grass groups, having the joint above the empty glumes as in the former but with the apical flower fertile as in the latter. The number of empty glumes is apparently four, but the upper two of these are to be regarded as the lemmas of two former florets, since one genus still possesses a spikelet of three flowers. The panic-grasses proper have been so regularly reduced to a single flower, often without vestiges of the second, that the various lines of evolution are not marked by clear-cut changes. The rice tribe constitutes an exception, since the spikelets are laterally compressed and the hilum is linear in contrast to conditions in the other five tribes, where the differences between the panics, zoysias, sorghums, and the relatives of corn are largely a matter of the grouping of the spikelets and the texture of the lemmas. Corn or maize stands by itself in consequence of the extreme specialization that has resulted in the ear, perhaps to be regarded as the outcome of long cultivation.

THE FLOWER CHART

Uses of the Chart

THE immediate value of the flower chart to the beginner as well as to the flower lover is to furnish an illuminated guide to the great group of flowering plants. It brings out clearly the chief features of interest, the starting point, the three great centers and the six main destinations, all of them located in regions of marked evolutionary activity. Between these lie secondary centers, which combine in varying degree the characteristics of the initial, central and terminal groups. This is not a matter of accident, but arises on the contrary out of a deep-seated community of origin, which affords the clue to the position and significance of each group. In consequence, the task set for the memory is enormously reduced, since each group foreshadows the next one, and all are strung together on the thread of cause and effect. This is the basis for the evolution of flowers—not a remote, vague or debatable process, but one in active operation today in field and garden everywhere. The chart renders evolution an intimate understandable operation, the evidences for which anyone can find for himself in his own garden, or in nature's garden. It is a graphic epitome of the problems that have confronted and still confront the working parts of flowers and of the various solutions that have been discovered.

The pressing need of each flower is for adequate pollination, and the chart with its formulae tells the story of increasing efficiency and success with a clearness and brevity possible in no other way. This is the driving force behind the changes that develop, and it serves to reveal the basic relationship in each great line of descent. Relationship is the open sesame to classification and the latter is one of the great tools of biological science, as well as one of vast service to mankind generally. But to achieve the maximum usefulness classification must have meaning, and this can come only from a study of evolution and

relationship as disclosed in the changes wrought by experience in the working parts of the flower.

Probably the greatest practical value of the chart lies in its use as a visual key to flowers. The usual printed key is the most valuable to those that need it least, and to the beginner especially it is as repellent as it is unusable. On the other hand, the chart stresses the earmarks of each order or famliy and the formula makes simple the task of comparing the essential features of related groups. Better still, each formula is a short-hand expression for the group concerned and furnishes by far the best means of attaining the goal sought by every interested student of flowers —the recognition of the family type upon sight.

Of the other values that can be derived from the flower chart one of the most interesting has to do with the uses to which man has put plants. This has already been noted in the case of the grasses, which furnish the chief food-supply of the world. Through specialization and increased parental care the seeds of the grains or cultivated grasses contain the largest and choicest store of flour—a fact of the greatest significance to man and one that he was not slow to discover. In other families success was secured by the production of an edible pulp attractive to birds and many four-footed animals. Such fruits proved equally attractive to man and he has exercised the utmost ingenuity in improving upon nature's handiwork in such families as the rose, with its edible apples, pears, quinces, peaches, apricots, plums, cherries, etc., the rue with the lemon, orange, grapefruit, lime, kumquat, and the gourd with melons, squashes, pumpkins, cucumbers, citrons, mangos, chayotes, etc. The mustards and capers are known for their pungent fruits and seeds, the parsleys for their fragrant seeds, and the walnuts for edible fruits—all illustrating a connection between relationship and use that recurs throughout the flowering plants.

The Use of the Chart as a Key

The flower chart was devised twenty-five years ago in consequence of the discovery that the family key of a manual was useless to the beginner and none too usable by many who were

not. Its first purpose was to serve as a ready and accurate guide to family characteristics or "types," and this has remained one of its chief uses. In the form employed in the present book, the formulae have been omitted for lack of space, but they have been supplied in the line charts (pp. 97, 108, 114). As a result the two must be combined in use, but this presents no serious difficulty since the search for a particular type proceeds along each main line. This is a consequence of the illuminating fact that such a line is essentially a unit in terms of origin, certain initial features of structure persisting throughout. Probably the best example of this is the number plan of 3, characteristic of the arrowhead-lily line and indelibly stamped upon practically all their descendants, even the most recent, such as the orchids and grasses.

The making of the formula is the first and the most important step in using the chart and in learning to recognize the family types. An inaccurate formula is worse than useless, and there is no royal road to an accurate one. However, if large flowers are employed at the outset, the only difficult task, that of determining the structure of the ovary, is easily mastered and it is then much simpler to do the same for small flowers. Two steps are necessary in each case; the first is to ascertain the exact number and arrangement of the four flower parts, and the next to express these in a formula. The meaning of the signs employed in the latter has already been given (p. 85), but it is repeated here for the sake of convenience.

The four parts are indicated by the first one or two letters as follows: calyx, Ca; corolla, Co; stamens, S; pistil, P. The four regular ways in which flowers are modified are (1) by changing the number of one or more parts; (2) by uniting the members of a part or the parts themselves; (3) by elevating parts, especially the corolla, and (4) by changing the form of parts, making the flower irregular. The number of members is designated by an exponent, e.g., Ca^5, S^{10}, variation by a dash between figures, as Ca^{3-5}, and an alternative number by the parenthesis, $S^{4(2)}$. Irregular parts are indicated by writing the numbers backward with a plus sign, thus Co^{3+2}, except where both calyx and corolla

are irregular, when the order is reversed for one. The sign ∞ is employed for a number greater than 20. The union of parts is denoted by a circle or for convenience in printing by a parenthesis. Union may operate upon any part, but it is most important in the case of pistil and corolla. Stamens especially may be partly united, either by their filaments or their anthers, and this is marked by a semi-circle, placed below in one case and above in the other. When the single pistils of the compound one separate at maturity or earlier, the circle is broken. In the case of most lilies and irids, the calyx and corolla are colored alike, a feature indicated by a tie drawn above them. In many cases, the four parts are found on essentially the same level and the four symbols are placed on the same line; in others, the corolla has become elevated with respect to the pistil and the latter is written below the line. Frequently the petals are joined to form a corolla tube and the stamens fuse with this so that they appear to be inserted on it, a condition indicated by a line above the corolla. Additional signs are employed for special cases in the complete chart with family formulae, but these need not be discussed here.

The formula once made, the usual procedure is to compare it with that of the buttercups on the "skeleton key" (p. 93). If it does not agree in the essential features, the next step is to read the three guide-posts for direction. If the flower plan is based on the number 3, the plant is a monocotyledon and must be sought along this line. If the number plan is 5 or the much less frequent 4, the choice must be made between the other two lines on the basis of the union of pistils into a compound one or the elevation of the corolla on the calyx cup. A united pistil is easily recognized by the number of styles or stigmas at its summit, or in doubtful cases by a section across the fruit or ovary to disclose the number of chambers, or "seams" in the wall. The slight elevation of the corolla in the simplest roses can usually be told by the tearing of the petal when pulled; it is lacking in the peas, but is easily recognized in the vast majority of the roses and their descendants.

The first step may be illustrated by means of the formula

for the larkspur, $Ca^{4+1}\ Co^{2+2}\ S^{\infty}\ P^{3}$. The most striking feature of the flower is its irregularity and the temptation is to jump at once to the conclusion that it represents a highly specialized type and to look for it among the mints or snapdragons. The proper procedure corrects this mistake at the outset, however, for the comparison with the buttercup formula shows the resemblance in the two essential parts, stamens and pistils. The number plan, though variable, indicates that the larkspur is not a monocotyl, a fact checked by the net-veined leaves. It exhibits no elevation and hence is not one of the rose group, though bearing a superficial resemblance to the pea flower. The pistils, though reduced in number, are not united and hence the green line, "Pistils United," cannot be crossed. In short, the larkspur is an irregular buttercup, the evidence of stamens and pistils being much more decisive than that of calyx and corolla, which change more easily.

From this trial may be derived one of the cardinal rules of the method, which is that the cross-lines must be passed in their proper order. In the case of the larkspur, it is not permissible to cross the lines for "Pistils United" and "Corolla United" in order to seek the flower among those above the line for "Corolla Irregular." Thus the cross-lines that mark the great steps in advancing efficiency for the insect-pollinated flowers of the solid lines serve equally well as sign-boards for the different regions. From the construction of the chart, they necessarily cross some of the broken lines of wind-pollinated flowers also, but they do not apply to them, since these regularly lack the corolla.

The common "butter-and-eggs" of the roadside may be employed to illustrate the use of cross-lines, the formula being $Ca^{(2+3)}\ Co^{\overset{S^{2+2}}{\overline{(3+2)}}}\ P^{(2)}$. The number plan shows that this is not a monocotyl, and the lack of elevation of the corolla that it does not belong in the rose line. In consequence, it is to be found somewhere along the buttercup-mint line. The union of the pistils carries it into the mallow-geranium region, but the united corolla takes it one step farther into the region of phloxes and gentians. It cannot belong here by virtue of the irregular corolla

and must be sought above this cross-line. Here the choice falls between snapdragons and mints, and the peculiar pistil of the latter determines that this flower must belong to the snapdragon order. In this are several closely related families, the decision between which must be made by means of a more detailed chart or by a manual. A comprehensive chart of all the families of North America and hence of much of the globe has long been in use, but cannot well be included in a brief general account. An example of the order charts that are employed as keys to each group of related families is given in the following section.

The use of the chart soon brings the realization that the same formula leads to a particular order or family. Each formula represents a "type" and in many cases this is so distinctive that the order is recognized as soon as the formula is completed without tracing it through the chart. With increasing acquaintance the type will come to be recognized by observing the main features of the floral structure without constructing the formula, and gradually the student will acquire the ability to recognize most of the common orders and families by the "look." One of the most distinctive types is that of the mustard family, with the formula $Ca^4\ Co^4\ S^{4+2}\ P^{(2)}$. The 4-plan of the flower is so characteristic that this family was long called "Cruciferae" or "cross-bearers." While there are other flowers with the number plan of 4, practically none have just the appearance of the mustards and the few that are confusing may be distinguished on the basis of the stamens. Occasionally, the latter will be S^{2+2} instead of the regular number S^{4+2}, but this is easily recognized as a mere variation of the normal plan. The pea flower is even more distinctive, with its formula $Ca^5\ Co^{2+2+1}\ S^{9+1}\ P^1$. Even when the stamens are grouped in different fashions, e.g., S^{5+5}, S^{10}, or $S^{(10)}$, or sometimes reduced in number, the form of the corolla is decisive. On the other hand, the stamen habit marks the genus *Amorpha* as a member of the pea family, although the flower possesses but a single petal, the "banner." The central or "name" family of most orders will gradually come to be recognized upon sight, and the related families can then be distinguished by

secondary earmarks within the order, as shown by the chart for the phloxes (p. 143).

How to Use the Chart Method in Teaching

The preceding discussion is intended for teachers and for nature-lovers generally, in short for those who must find their own way. It is not designed for students in regular courses, who should be given the opportunity to discover the path for themselves. The study of flower relationships and evolution is one of the best of all fields for encouraging and developing the spirit of inquiry, and none of the traditional methods of teaching, such as the use of textbook or lecture, should be permitted to destroy this greatest of all values.[1]

It is obvious from the outset that the chart method demands the use of living material. In the study of life and its processes this would seem self-evident were it not for the difficulties that appear to excuse if not to justify the use of dried or preserved specimens, of "mummies and pickles." Nearly all these difficulties center about the school year, which includes all of the year when flowers are not available in field and garden, except in favored climates. The problem can be solved by having the study of flowers carried on in the spring, where this includes two or three months at least. A briefer period can hardly be expected to yield usable or permanent results. Much the best plan is to rely upon garden and greenhouse and to utilize the field as far as season and schedules render possible. In fact, it must be realized that in all large cities and many others, field excursions are practically out of the question, and that first-hand contact with the plant world during the school term can be secured only through garden and greenhouse. No matter what it may be called, whether botany, nature-study, general science or biology, the study of life without adequate living material is a travesty, and under such conditions it should not even be attempted. A community that regards a knowledge of life processes as essential to living

[1] F. E. Clements, 1911: Methods of botanical teaching, *Science* 33: 642; 1923: The ecological method in teaching botany. Content, methods and measurements in the teaching of elementary botany, *New Phyt.* 22: 98, 105.

will find no serious difficulty in providing the facilities for this, though its duty in this respect may need to be pointed out by a teacher of earnest conviction.

The best approach to the work of flowers and to their experience as recorded in their structure is a garden much frequented by bees, butterflies and other pollinators. A study garden should have a good range of families and species, a wealth of individuals and a succession of bloom. Each student should select his own species and plant, or a group may choose to work on different individuals of one species in order to permit a more exact comparison of results. In order to follow the daily round in detail for several days, it is best to form the group from several sections when possible, selecting one student from each. This is also desirable, though less essential, in following the course of pollination. The first period in the garden may well be devoted to the task of having each one determine for himself how far he can go independently in discovering the work of the flower and its parts. With this as a basis, the class can work out a more or less uniform plan under the guidance of the instructor and apply it to the investigation of the daily round of behavior and the details of pollination as exemplified by the different types of visitors.

With a working knowledge of the rôle of each flower part, of the life of the flower from bud to fruit and of the detailed procedure in pollination, each student is equipped to begin the study of structure. For obvious reasons the best types for a beginning are to be found in the buttercups, or in one of the three centers. The details of the initial flower once worked out and expressed in a formula, a second type is studied in the same manner. The two formulae now make a careful comparison possible and furnish the essential method in building the chart. The most satisfactory procedure is to have available flowers representing the cardinal points of the chart, namely, the beginning, the three centers and the six ends, but this is possible with unusual facilities only. However, it is feasible to have material of the buttercup, lily, rose and geranium orders at several seasons of the year, as well as types that show the characteristic

advances exemplified by union, irregularity and marked elevation of the corolla.

With the formula of the buttercup or a center type as a standard, it is possible to determine the amount of difference shown by any other type, and hence its degree of advance or specialization. The observations in the garden will have prepared the students to decide that one stigma is more readily and certainly pollinated than many, that the union of pistils and of petals brings about an economy of material, and that an irregular corolla affords advantages in the way of landing, guidance and effective pollination that are lacking in a regular one. In all of this, there will necessarily be frequent opportunity for guidance by the teacher, but this should always be suggestive merely, leaving decisions and reasons for them to the students individually and as a group. With the relative position of several points fixed, it becomes an increasingly simple matter to locate new types and thus to complete the chart to any degree that time and interest permit.

In the orders that are well represented in a region, the class should be encouraged to construct charts for the families dealt with. These are likewise based upon the family formulae, but these must sometimes be extended to include additional features, such as the number of ovules in each cell of the ovary, the folding of the corolla in the bud or estivation, the attachment of the ovules, the character of the leaves, etc. In the original family chart most of the general characters were indicated by initials or abbreviations placed below a line drawn beneath the entire formula. This additional information as to the life-form, whether tree, shrub or herb, the leaf, fruit, etc., is always helpful, though hardly necessary in orders where families are distinguished primarily upon flower characters. This may be illustrated by the phlox order, which is one of the best represented in this country.

A comparison of the formulae for the five families of this order discloses the fact that the chief differences lie in the number of cells in the ovary and the number of ovules in each cell. The general number plan is sometimes 4 instead of 5, but this

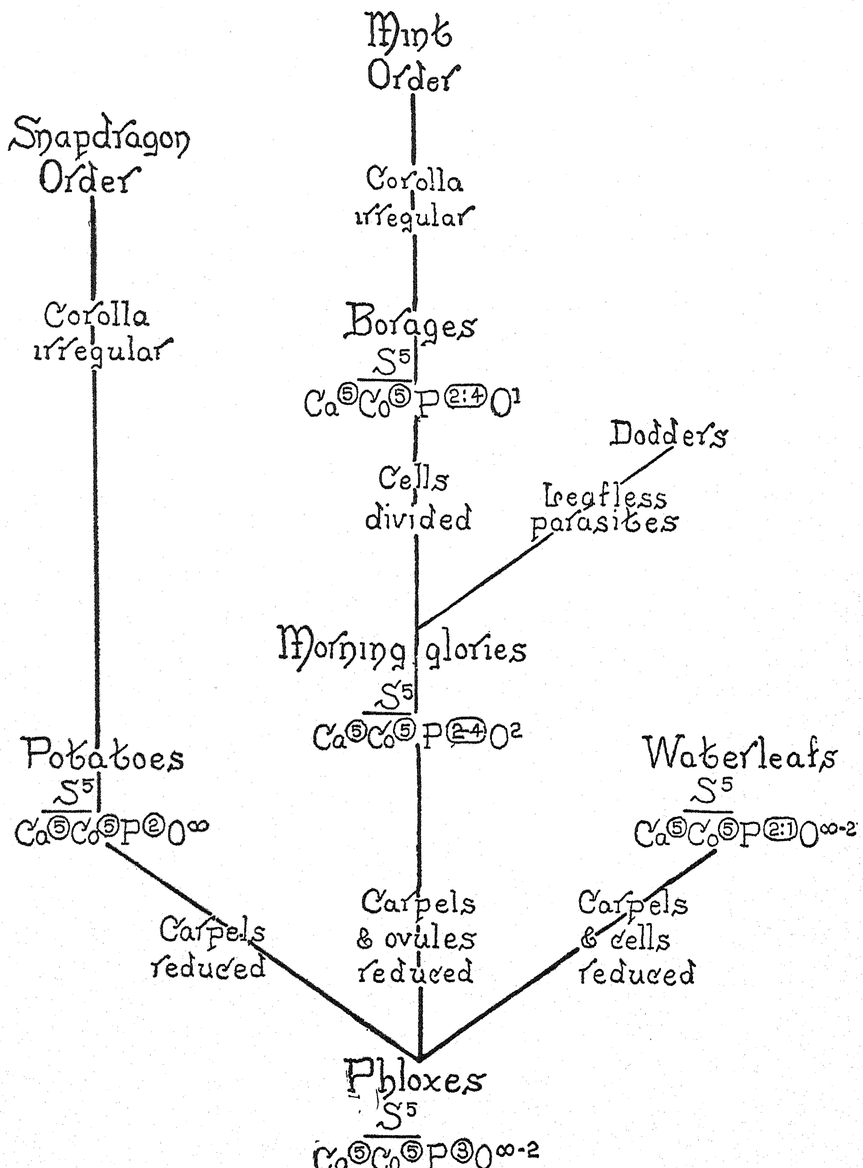

FIG. 64. FAMILY CHART OF THE PHLOX ORDER

variation is unimportant, since it may occur in any of the families. There are occasionally odd numbers in the pistil, such as a rare ancestral 5 for the phloxes, but these are infrequent exceptions. However, this 5-celled pistil is important in confirming the position assigned the phloxes by virtue of its typically 3-celled pistil. As with all flower parts, reduction in number is a mark of efficiency, and hence of specialization and advance. The phlox pistil offers three possibilities of reduction, namely, decrease in the number of carpels, of cells, or of ovules. Each of these possibilities has been realized and the consequence has been three corresponding lines of development, resulting in as many different families, the potatoes, morning glories and waterleafs.

In the potato family the carpels have been decreased to 2, but the ovules remain numerous. The morning glories have reduced both ovules and carpels to 2, the number 4 resulting from a subsequent division of the two cells, while the waterleafs have not changed the ovules but have typically suppressed the partition in the ovary, thus fusing the two cells into one. The morning glories have in turn given rise to two new lines; one of these has operated within the typical flower structure, but has modified the plant-body profoundly. This has produced the dodders, which are leafless parasites with little or no green coloring matter or chlorophyll. In the other direction, the tendency to divide the two cells of the ovary has become fixed, and this has resulted in four 1-seeded nutlets, typical of the borages and their descendants, the verbenas and mints. Certain of the borages foreshadow the next great change by the possession of a somewhat irregular corolla, as do some members of the potato family likewise. As this change develops, the borages pass into the mint order, and the potatoes into the snapdragon order.

Classification and Names

The name of a plant consists of two terms or words, as, for example, *Viola pedata, Aquilegia coerulea, Calochortus venustus,* and hence is spoken of as a binomial. The first word indicates

the *genus* and is always capitalized; the second word designates the kind or *species* and as a rule is not capitalized. The meaning of the term *genus* (plural, *genera*) and *species* (plural, *species*) may be illustrated by the columbines and violets. The red, blue, and yellow columbines are different kinds or *species* of the *genus* of columbines, which is called *Aquilegia;* each one is designated by a species name, *canadensis, coerulea,* and *chrysantha,* respectively. The blue violet, yellow violet, and white violet are different species of the violet genus, *Viola;* they are distinguished by the respective species names, *pedata, biflora,* and *blanda.*

As we have already seen, genera that are related to each other are placed in one *family;* for example, anemones, buttercups, columbines, clematis, larkspurs and monkshoods all belong to the buttercup family, *Ranunculaceae.* Asters, daisies, goldenrods, sunflowers, thistles, dandelions and ragweeds are members of the aster family, *Asteraceae.* The ending *-aceae,* which is always used to denote a family, is the feminine plural of the Latin suffix, *-aceus,* meaning *like* or *related to.* The family name, *Asteraceae,* is really an adjective agreeing with *plantae,* plants, and signifying "plants related to the aster." Related families are grouped into orders, which also bear a distinctive ending, e.g., *Asterales, Ranales.* This form is likewise in the feminine plural, and the meaning of the name is "plant families related to the aster family," etc. Finally, orders are arranged in larger groups or classes.

Wild Gardens and Flower Conservation

The study of plants as living working organisms leaves no place for student collections of dried plants, the so-called "herbaria" of school and college. These rarely if ever yielded an adequate or permanent return in the knowledge of plant names or relationships, and they were especially unfortunate in taking the emphasis away from the study of living things. Moreover, they often took a heavy toll of native species, the beautiful or rare species suffering the most, even to the point of extinction locally. While the purpose was different, the

effect was much the same as that of the armfuls of wild flowers plucked by the thoughtless or the indifferent, or wantonly destroyed by the vandal. The destruction of wild flowers has been greatly augmented by the facility with which the motorist can reach their haunts and many a country road has been despoiled of its treasures. Something has been accomplished by the Wild Flower Preservation Society in molding public opinion and by statute and ordinance, but much more is yet to be done.

From the standpoint of direct conservation as well as of education, the wild garden is probably unique in its effectiveness. It not merely saves the rare and beautiful species from extinction by giving them the protection of the garden, but it has even provided a supply of seeds by which they may again be restored to their place in nature. Even more important is the growing sense of acquaintanceship and sympathy for wild flowers, and a greater appreciation of the rights of living things. For teaching and learning in the vital human sense, by daily contact with life itself, the wild garden may surpass the cultivated one, since it often serves as the student's only effective approach to nature.

Just as every school should have a greenhouse and a cultivated garden, so should it also have a wild garden. This can best be organized and developed by the students themselves under the guidance of the teacher. Much the most attractive plan is that of community groups, in which the various species are associated to form miniatures of the natural plant communities of the region, such as pond, meadow, prairie, thicket and woodland. In the case of perennials where the natural supply warrants, transplants may be moved into the garden directly and much insight obtained into the housekeeping arrangements of the various species. With practically all annuals and many perennials, as well as woody plants, it is simpler to grow the plants from seed. This should be collected by the students themselves under proper instructions, where opportunity permits, though seasons and schedules often render this difficult or impossible. Fortunately, there has been a slow but

steady growth in the appreciation of wild-flower gardening as a consequence of the interest of a few devoted leaders, and seeds of an increasing number of native species are now available.[1]

[1] In California and for the Pacific Coast generally, seeds, bulbs, and plants of native species can be obtained from Theodore Payne, Los Angeles, and Carl Purdy, Ukiah, California. Natives of the Rocky Mountain region are listed by D. M. Andrews, Boulder, Colorado, and those of the East in general by Harlan P. Kelsey, Salem, Mass., Edward Gillett, Southwick, Mass., Wayside Gardens Company, Mentor, Ohio, and Wild Flowers Company, Rose City, Michigan.

LEGEND FOR FIG. 28, ON PAGE 45

FIG. 28. FLOWERS AND THEIR VISITORS

(1) Ruby-throated Hummingbird and Hummingbird-trumpet; (2) Blue Sage pollinated by bee; (3) Snapdragon; (4) Bee escaping from pouch of Lady-slipper and rubbing against an anther; (5) Butter-and-eggs; (6) Yucca flower being pollinated by Pronuba moth; (7) Sphinx moth with long sucking tube; (8) Bee on flower of horse-chestnut; (9) Bettle on Tway-blade; (10) Honey-bee in violet; (11) Leg of bee with pollen basket: a, empty; b, loaded with pollen.

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